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TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 31, Number 1 1 November 1999

OBSERVATIONS ON THE NINE-BANDED ARMADILLO, *DASYPUS NOVEMCINCTUS*, IN SOUTHERN LOUISIANA

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SYSTEMATIC REVIEW OF SUBGENUS *FUSCATELUM* OF *ETHEOSTOMA* WITH DESCRIPTION OF A NEW SPECIES FROM THE UPPER BLACK WARRIOR RIVER SYSTEM, ALABAMA

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FUSCONAIA APALACHICOLA, A NEW SPECIES OF FRESHWATER MUSSEL (BIVALVIA: UNIONIDAE) FROM PRECOLUMBIAN ARCHAEOLOGICAL SITES IN THE APALACHICOLA BASIN OF ALABAMA, FLORIDA, AND GEORGIA

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TULANE STUDIES IN ZOOLOGY AND BOTANY
ISSN 0082-6782
Tulane University Museum of Natural History
Building A-3, Wild Boar Road
Belle Chasse, Louisiana 70037

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ABSTRACT

From 1970 to 1995, observations were made on the nine-banded armadillo, *Dasypus novemcinctus*, in southern Louisiana at the Riverside Campus of Tulane University. Observations and corresponding data were obtained on natural history in general, with emphasis on home range, as well as development and growth of young, in particular.

INTRODUCTION

Although a considerable amount of information has been amassed on the ecology and life history of *Dasypus novemcinctus* (McBee and Baker, 1982), we present herein some additional data from a long-term study of the species conducted in southern Louisiana.

Lowery (1936) recorded range extensions of *D. novemcinctus* within Louisiana. Most of his records were from west of the Mississippi River. However, he mentioned that in late December 1935, two armadillos were captured south of Baton Rouge east of the Mississippi River. Later, Lowery (1943) stated that armadillos were abundant in southwestern Louisiana and that they were common in most of the western portions of the state, but that these mammals were encountered infrequently east of the Mississippi River in the Florida parishes. Fitch et al. (1952) presented many distributional records for the armadillo in Louisiana, Arkansas, and Mississippi, but they had no records for either the Louisiana coastal marshes or the lower Mississippi River delta area. Lowery (1974) included a distribution map based on museum specimens; his record for the delta region just southeast of New Orleans was based on specimens in the Museum of Natural History of Tulane University. For their distribution map of the armadillo, Choate et al. (1994) included all of coastal Louisiana, except for the extreme lower end of the Mississippi River delta and adjacent marshes on both sides. We postulate that *D. novemcinctus* may have gained early access to the lower Mississippi River delta by moving down along the Mississippi River levees.

It is of interest that the earliest specimen of *D. novemcinctus* deposited in the collection of mammals of Tulane University was obtained on 14 January 1966. However, based on our observations, as well as those of other personnel of the

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University, armadillos were reported as common at the Riverside Campus since 1964.

The purpose of this paper is to present summaries of our observations of *D. novemcinctus* in southern Louisiana. Published literature pertinent to our findings is reviewed. However, for a more extensive list of the literature on this species, see the work by McBee and Baker (1982).

STUDY AREA. The Riverside Campus of Tulane University is a 520-acre tract of land at the northern end of Plaquemines Parish, several miles southeast of New Orleans, Louisiana (Figure 1). The area is west of the Mississippi River at English Turn Bend (river mile 78). The Mississippi River forms the southern boundary of the Riverside Campus. More than 1,000 acres of bottomland hardwoods are adjacent to the eastern and northern boundaries of the property.

During World War II, ammunition storage bunkers were constructed throughout the central part of the current Riverside Campus. Throughout the entire area, inclusive of the adjacent acreage, a system of drainage ditches was excavated, and the soil was piled along the ditches. Many of the ditches date back to the early plantation days typical of the area. In subsequent years, trees (*Celtis laevigata, Acer negundo, A. rubrum, Carya illinoensis, Salix nigra, Ulmus americana, Populus deltoides, Quercus virginiana, Myrica cerifera*, and *Sambucus canadensis*, to name some of the common species) became established along and on these spoil ridges alongside the drainage ditches. In the adjacent wooded areas, there are stands of scattered individuals of *Taxodium distichum, Quercus nuttali, Q. nigra, Morus rubra, Magnolia grandiflora, Liquidambar styraciflua, Platanus occidentalis, Diospyrus virginiana, Gleditsia triacanthos, Salix interior, Cephalanthus occidentalis, Nyssa aquatica*, and *Fraxinus pennsylvanica.*

Some of the excavated dirt was piled on and around the ammunition storage bunkers for camouflage; this resulted in the formation of extensive series of ponds (Figure 1-B). The elevated spoil banks along ditches and the elevated soil slopes around the bunkers have become ideal burrowing sites for armadillos. Moreover, the drainage system that was developed during the plantation days and enhanced further by development of the ammunition storage facility resulted in the lowering of the water table and the eventual collapse of soil around the bases of large trees, thus providing additional sites for burrowing by armadillos.

A detailed description of the ammunition storage bunkers was provided by Jones and Pagels (1968). Warkentin (1968) briefly described the common vegetation around the ponds (borrow pits). Suttkus and Jones (1991) described the Riverside Campus of Tulane University and adjacent wooded areas, and provided a list of the common trees on the area. During about the last five years, two invading plants have become abundant in the area. The wind-blown seeds of the Chinese tallow (*Sapium sebiferum*) have germinated on the bare, moist soils along the edges of the ponds during low water levels. It seems that birds have spread the seeds of the Chinese privet (*Ligustrum sinense*) into the area; now most of the margins of the wooded areas are crowded with privet.

During the early to late 1960s, the railroad tracks along the fronts of the ammunition storage bunkers were removed. The railroad track right-of-ways were converted to shell roadways. In addition, most of the brush and trees from on top

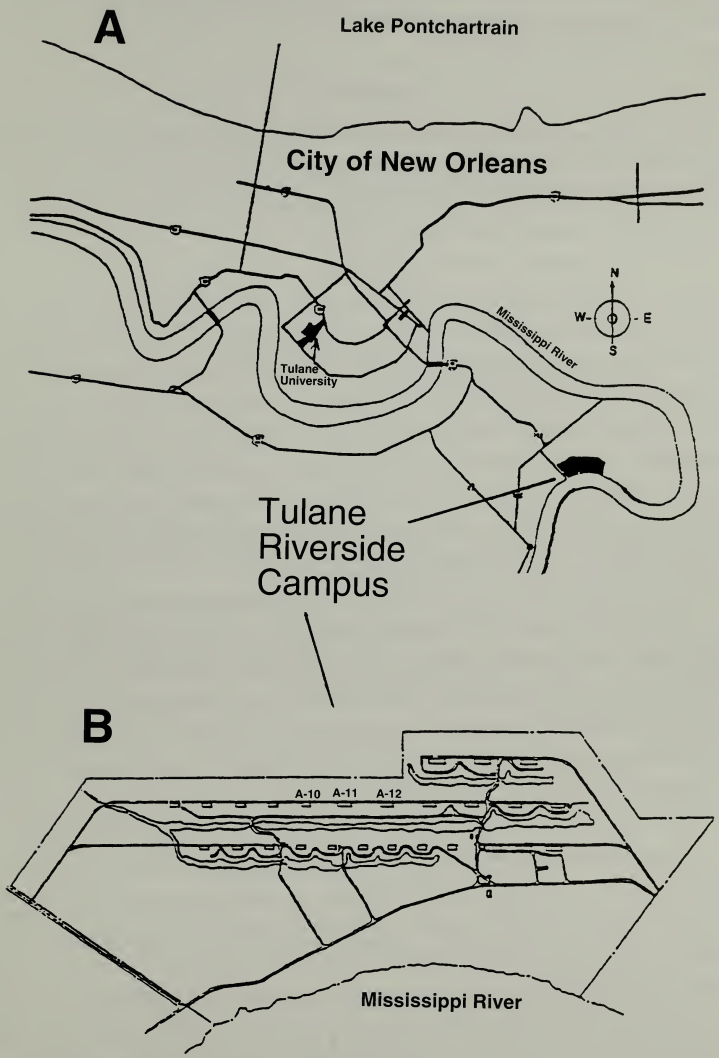

Figure 1. Location of the study area (Riverside Campus of Tulane University) in southern Louisiana. A. General location; B. Enlargement of Riverside tract.

of and around the bunkers were removed. The resultant, open, mowed areas became foraging grounds for armadillos, in addition to the diversity of foraging areas in the adjacent wooded areas.

Methods

Our methods of capture and marking armadillos were similar to those used by Clark (1951), Fitch et al. (1952), and Breece and Dusi (1985), except that instead of numerals, we sprayed a polka-dot pattern on the animals. We captured the animals either by hand or more often with a deep, large-mesh, nylon, long-handled net. We made stencils of cardboard with holes (quarter size) that we used to transfer a polka-dot pattern to the scapular or pelvic shield (or both) with different colors of fluorescent spray paint. The same patterns, numbers, and colors were painted on the right and left side of each animal. During the course of the study, some armadillos were repainted when either one side or the other started to fade. In addition to the spray-paint spots, each animal was tagged on the left ear pinna with a small fisheries opercular strap tag. For nearly all of the armadillos, total length in millimeters (mm), weight in kilograms (kg), and sex were recorded at the time of capture, marking, and tagging.

Armadillos captured initially near the ammunition storage bunkers were marked accordingly. Animals captured near bunker A-9 were marked with yellow; those from the bunker A-10 area were marked with purple; armadillos from around bunker A-11 were marked with green; those from near bunker A-12 were marked with red; animals captured near bunker A-13 were marked with blue; those from around bunker A-14 were marked with gold; and those from the areas adjacent to bunkers A-1, A-2, and A-3 were marked with white.

Animals were marked, tagged, and the corresponding data were recorded at the site of capture; upon completion of the process, the armadillos were released. Most of the *Dasypus* were captured initially and marked on the following dates (numbers of animals in parentheses):14 February 1970 (17); 17 February 1970 (3); 18 February 1970 (8); 22 February 1970 (6). No new armadillos were captured and marked after 22 February 1970. Approximately half of the animals (23) used in the computations of home ranges were recaptured and remarked during the aforementioned period of observations. Identity of each individual remarked was verified by the number of the ear tag.

Some observations of animals were made with the use of field binoculars. However, most of the spray-paint markings could be observed easily with the naked eye. Each observation of a marked armadillo was plotted on a ground chart of known scale. In addition, the time of day, air temperature, and presence and location of other marked, as well as unmarked, animals were recorded. After 14 February 1970, observations were continued periodically throughout March and most of April of 1970.

In this study, minimum home ranges of *D. novemcinctus* were calculated in the manner described by Clark (1951). Each observation of a marked animal was plotted on a known-scale ground chart. The outermost points of the observed ranges of the animals were connected by straight lines; thus, the minimum home range was circumscribed. The minimum home range in acres was determined by placement

of a grid over the known-scale ground chart, counting the number of whole squares within the range diagram, and adding the whole-square equivalent to all of the partial enclosed squares.

Materials for the study of development were obtained by salvage of animals dead on the roads or from females captured in the area. All embryos were deposited in the Tulane University Museum of Natural History as were the salvageable females (mothers). Measurements to the nearest 0.1 mm were taken with a dial caliper.

Additional observations on various aspects of life history and other activities of *D. novemcinctus* in the study area and adjacent regions were carried out sporadically from February 1970 through the fall of 1995.

Results

Home Range and Movements.—A total of 34 armadillos (20 males, 14 females) was captured and marked during this study. After the initial capture, three males and two females were not seen again. One male and one female were observed only one time after being marked. One male and three females were observed two times after the initial capture. Information from these 11 individuals was not used in the determinations of home ranges. Throughout most of the study, especially in the 1970s and 1980s, some armadillos were found dead from apparent gunshot wounds. For example, three animals were found dead after 12, 14, and 12 days of observations, respectively. Minimum home ranges were determined for 14 males and nine females (Table 1). Home range overlap was common; overlaps of ranges of marked animals are presented in Table 2. There were fifteen periods of observations during 17–28 February 1970. Beginning times of observation periods ranged from 1010 to 1722 hours, air temperatures during these observation periods ranged from 14°C to 23°C, with a mean of 17.9°C. There were 22 periods of observations during 1–28 March 1970. Beginning times of observation periods ranged from 1015 to 1800 hours, with air temperatures that ranged from 12°C to 23.5°C with a mean of 17.9°C. Whether the mean temperature of 17.9°C for the 15 observation periods in February and the 22 observation periods in March was coincidental or whether the animals were highly sensitive to air temperatures and regulated their above ground activities accordingly we are not prepared to say. There were two observation periods in April (12 April 1970; 1445 hrs.; 17 April 1970; 1735 hrs.). Air temperature was 25°C during both observation periods.

Development.—Data on seven litters of armadillos from five different years were obtained from the study area. Three of the females carrying fetuses were found dead on roads; four pregnant females were caught by hand. The aforementioned female armadillos were obtained on 15 April 1970, 10 March 1982, 11 February 1983, 14 February 1986, 7 March 1986, 28 February 1987, and 15 March 1987. As expected, all litters included four fetuses. For convenience of presentation, the data presented in Table 3 are arranged by average sizes of fetuses rather than chronology of capture.

Discussion

Home Range and Movements.—Some early work on home range of *D. novemcinctus* was conducted in southern Texas by Clark (1951). Between 18 October 1947 and 15

Table 1. Minimum home ranges and related data for 23 armadillos in southern Louisiana.

Tag Number	Sex	Weight (kg)	Total Length (mm)	Number of Observations	Days of Observations	Minimum Home Range	
						Acres	Hectares
428	Male	4.2	730	8	35	0.89	0.36
460	Male	2.75	710	5	35	0.59	0.24
461	Male	2.75	710	4	12	0.39	0.16
432	Male	4.5	775	14	22	1.67	0.68
434	Male	4.5	735	25	39	2.86	1.16
435	Male	—	—	7	23	0.74	0.30
459	Male	5.0	840	12	55	1.15	0.46
464	Male	3.4	712	6	15	1.08	0.44
441	Male	4.25	720	10	14	1.33	0.54
442	Male	—	—	10	16	2.31	0.93
447	Male	—	725	14	12	1.47	0.59
448	Male	—	660	15	18	2.15	0.87
449	Male	4.0	740	19	21	3.58	1.45
465	Male	3.25	760	6	8	0.39	0.16
457	Female	3.25	635	9	17	1.74	0.70
429	Female	5.5	835	9	12	0.64	0.26
431	Female	4.5	750	11	43	1.92	0.78
433	Female	5.0	790	23	63	2.32	0.94
454	Female	3.5	727	8	19	0.57	0.23
436	Female	3.5	705	7	9	0.54	0.22
439	Female	2.0	—	12	25	1.94	0.78
450	Female	4.5	750	11	21	1.99	0.80
451	Female	3.5	735	4	25	3.32	1.34

February 1948, surveys to observe armadillos were made 30 times. Four animals (one juvenile, three adults) were observed on more than four occasions. The longest period of observation was 28 days. It was estimated that the juvenile armadillo had a home range of 0.69 acres (0.3 hectares, ha); the three adults had an average home range of 8.5 acres (3.5 ha).

From February to June of 1948, Fitch et al. (1952) studied home ranges of armadillos in Natchitoches Parish, Louisiana. Based on 32 observations of 13 different animals, they concluded that the usual home range of an individual was approximately 50 acres (20.3 ha).

Layne and Glover (1977) marked and released 47 armadillos in Highlands County, Florida. They presented estimates of minimum home ranges for eight of 12 animals that were observed four or more times between July 1968 and September 1974. Their estimates of home ranges of *D. novemcinctus* varied from 2.72 acres (1.1 ha) to 34.10 acres (13.8 ha), with an average of 14.08 acres (5.7 ha). In addition, Layne

Table 2. Tag numbers and sexes of free-ranging armadillos with overlapping home ranges in southern Louisiana.

Number, Sex	Number, Sex of Armadillos with which Home Ranges Overlapped
428, male	457, female; 460, male; 461, male
429, female	457, female; 434, male; 461, male
431, female	432, male; 434, male; 433, female; 435, male; 454, female; 459, male
432, male	431, female; 434, male; 433, female; 435, male; 454, female; 459, male
433, female	431, female; 432, male; 434, male; 435, male; 454, female; 459, male
434, male	429, female; 431, female; 432, male; 433, female; 435, male; 454, female; 459, male
435, male	431, female; 432, male; 434, male; 454, female; 459, male; 441, male
436, female	459, male; 464, male; 441, male; 442, male
439, female	441, male; 442, male
441, male	459, male; 436, female; 439, female; 442, male
442, male	439, female; 441, male
447, male	449, male, 451, female
448, male	449, male; 450, female
449, male	447, male; 448, male; 450, female
450, female	448, male; 449, male
451, female	447, male
454, female	431, female; 432, male; 434, male; 433, female; 435, male; 459, male
457, female	428, male; 460, male; 461, male; 429, female
459, male	433, female; 435, male; 454, female; 464, male; 436, female; 441, male
460, male	457, female; 428, male; 461, male
461, male	457, female; 428, male; 460, male
464, male	435, male; 454, female; 459, male
465, male	No overlapping home ranges with any marked armadillos

and Glover (1977) provided information on sizes of animals. The mean weight for 12 armadillos was 2.7 kg; the largest male weighed 3.4 kg and the largest female weighed 3.8 kg.

Thomas (1980) fitted a transmitter to an adult male *D. novemcinctus* in Bosque County, Texas. The animal weighed 5.0 kg when captured; the weight was 4.7 kg at the time of release five days later. The animal was released on 4 June 1978 and located 43 times during a period of 55 days. Based on the minimum polygon method, the home range was estimated at 20.01 acres (8.1 ha).

Galbreath (1982) reported information on home ranges of two adult armadillos (one male, one female) at the Archibold Biological Station, Highlands County, Florida. The size of the home range of the male was estimated at 26.69 acres (10.8 ha); that of the female was 18.78 acres (7.6 ha). Galbreath (1982) also included some information on estimated sizes of home ranges of 8.15 acres (3.3 ha) for males and 8.40 acres (3.4 ha) for female armadillos at an unspecified site in Mississippi.

Table 3. Morphometrics (mm) of seven sets of fetuses of armadillos from southern Louisiana. Means are in parentheses. See text for dates of collections and descriptions of fetuses.

Total Length	Tail Length	Hind Foot	Ear	Head Width	Scapular Shield Width	Scapular Shield Length	Pelvic Shield Width	Pelvic Shield Length	Head Length	Trunk Length
Set 1										
21.0	11.7	3.2	2.0	6.7	8.2	7.4	7.8	6.1	11.5	15.5
21.0	12.2	3.5	2.3	6.6	8.3	7.5	7.6	6.9	11.5	15.5
20.8	12.4	3.4	2.1	6.3	8.3	7.1	7.5	6.3	11.5	15.6
21.0	12.0	3.3	2.0	6.5	8.7	7.0	6.7	6.5	11.2	16.7
(21.0)	(12.1)	(3.4)	(2.1)	(6.5)	(8.4)	(7.3)	(7.4)	(6.5)	(11.4)	(15.8)
Set 2										
34.8	16.5	6.8	3.2	9.0	13.7	10.1	12.0	9.1	15.8	27.2
34.8	16.4	7.0	3.5	9.4	14.5	10.7	12.5	9.2	15.5	27.5
33.6	16.2	6.9	3.2	9.1	14.1	10.4	13.5	8.8	15.0	26.8
34.3	16.5	7.2	3.6	9.5	14.5	10.8	13.4	8.3	15.5	27.4
(34.4)	(16.4)	(7.0)	(3.4)	(9.3)	(14.2)	(10.5)	(12.8)	(8.9)	(15.5)	(27.2)
Set 3										
84.0	29.0	9.0	4.0	12.5	14.3	13.4	13.6	11.8	23.2	36.2
88.0	28.0	9.0	4.0	12.4	14.0	16.8	16.3	11.8	22.6	36.1
86.0	28.0	9.0	4.0	12.1	13.7	14.9	14.8	11.6	23.4	36.5
87.0	30.0	9.5	4.0	12.2	14.3	15.5	16.5	12.0	23.5	37.0
(86.0)	(29.0)	(9.1)	(4.0)	(12.3)	(14.1)	(15.2)	(15.3)	(11.8)	(23.2)	(36.5)

7 March 1986										
87.5	27.5	10.1	3.7	13.3	—	13.9	—	12.6	22.8	39.3
88.6	29.1	10.7	3.8	12.8	—	13.9	—	13.1	23.7	39.5
85.6	27.5	10.8	3.8	13.9	—	14.9	—	13.5	24.4	41.3
85.6	28.0	10.3	3.8	12.7	—	14.2	—	13.3	23.7	39.5
(86.4)	(28.0)	(10.5)	(3.8)	(13.2)	—	(14.2)	—	(13.1)	(23.7)	(39.9)
Set 4										
120.0	44.0	17.0	8.0	17.0	26.7	15.2	27.5	18.8	32.6	50.6
119.0	44.0	16.0	8.0	16.2	24.8	15.2	27.0	18.6	33.3	51.5
120.0	44.0	17.0	8.0	17.6	26.0	15.2	26.5	18.5	32.9	50.8
115.0	44.0	17.0	8.0	17.4	26.0	15.2	26.8	18.8	33.2	50.3
(119.0)	(44.0)	(17.0)	(8.0)	(17.1)	(25.9)	(15.2)	(27.0)	(18.7)	(33.0)	(50.8)
Set 5										
153.0	53.0	22.0	11.0	20.0	27.3	19.0	28.4	24.5	37.1	61.4
152.0	54.0	20.0	10.0	18.2	28.0	18.0	30.7	25.2	37.1	63.2
152.0	52.0	20.0	11.0	19.8	28.0	18.0	29.2	24.4	36.3	63.0
153.0	54.0	21.0	12.0	19.2	27.3	18.1	27.8	24.5	37.2	60.3
(153.0)	(53.0)	(21.0)	(11.0)	(19.3)	(27.7)	(18.3)	(29.0)	(24.7)	(36.9)	(62.0)
Set 6										
241.0	105.0	35.0	19.0	24.8	33.2	25.1	36.5	34.3	51.1	90.7
242.0	100.0	39.0	19.0	25.5	34.6	23.0	37.0	32.5	51.5	96.5
240.0	101.0	34.0	19.0	24.8	32.2	26.2	33.5	32.0	52.0	92.5
242.0	101.0	35.0	19.0	24.5	32.2	25.6	34.2	32.2	52.5	93.5
(241.0)	(102.0)	(36.0)	(19.0)	(24.9)	(33.1)	(25.0)	(35.3)	(32.8)	(51.8)	(93.3)

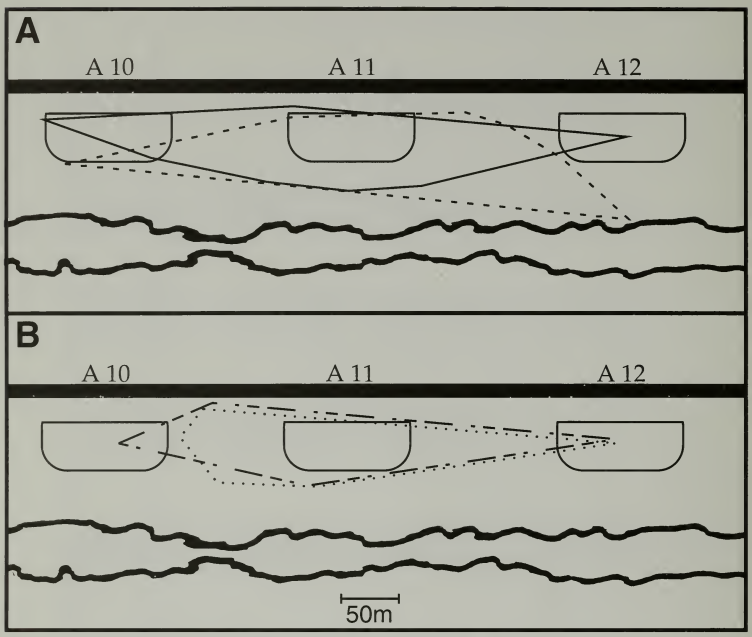

Figure 2. Enlargement of area around bunkers A-10, A-11, A-12 showing bunkers in relation to shell road (heavy black line) and long pond. A. Home ranges of female, number 433 (———) and male, number 434 (- - -); B. Home ranges of female, number 431 (— — —) and male, number 432 ( ).

Breece and Duci (1985) observed 26 adult and 26 juvenile, marked armadillos at the Fred T. Stimpson Sanctuary in Clarke County, Alabama, from July 1972 through August 1973. Average minimum sizes of home ranges for 21 adults seen three or more times each were estimated at 8.67 acres (3.5 ha), whereas those of 15 juveniles were 3.63 acres (1.5 ha).

Based on our observations of *D. novemcinctus* in southern Louisiana, estimates of sizes of home ranges were smaller than those presented in the aforementioned studies. Our estimates were derived by using the minimum polygon method for data obtained on 23 of the original 34 armadillos that were marked and released during the study. Number of observations per individual ranged from four to 25; duration of observations per individual ranged from eight to 63 days (Table 1). Estimated minimum home ranges for 14 males varied from 0.39 acres (0.2 ha) to 3.58 acres (1.4 ha), with a mean of 1.47 acres (0.6 ha). Similar estimates for nine females varied from 0.57 acres (0.2 ha) to 3.32 acres (1.3 ha), with a mean of 1.66 acres (0.7 ha). Analyses of combined data for 14 males and nine females resulted in average,

estimated, minimum home ranges of 1.55 acres (0.6 ha).

There were no apparent correlations between sizes of armadillos and estimated sizes of home ranges. For example, the smallest, marked animal in our study was a female (tag no. 439; 2.0 kg) that was observed on 12 occasions over a period of 25 days; she had an estimated home range of 1.94 acres (0.8 ha). A large, marked female (tag no. 431; 4.5 kg) that was observed 11 times during a period of 43 days had an estimated home range of 1.92 acres (0.8 ha). Figure 2-A depicts the home range of a female, tag no. 433; 5.0 kg; 790 mm total length (TL), based on 23 observations during a period of 63 days and a male, tag no. 434; 4.5 kg; 735 mm TL, based on 25 observations during a 39 day period.

Figure 2-B depicts the home range of a female, tag no. 431; 4.5 kg; 750 mm TL, based on 11 observations during a period of 43 days and a male, tag no. 432; 4.5 kg; 775 mm TL, based on 14 observations during a period of 22 days (Tables 1 and 2).

Obviously the home ranges of the four armadillos cited above overlapped considerably and so it was impractical to place all four on the same diagram. Moreover, there were two additional females and two additional males that had overlapping home ranges with one or more of the four foregoing listed animals (Table 2). These latter four animals also had elongate home range patterns similar to those shown in Figure 2-A and 2-B.

The small sizes of our estimated home ranges of armadillos may be correlated with the topography of the study area, as described previously (Figure 1). The abundance of relatively well-drained burrowing sites seemingly was important to the animals in the area. Hard-packed roads may have served as partial deterrents to movements of animals, especially when foraging. However, it was not uncommon to see armadillos crossing roads. During this study, marked animals frequently were observed foraging in open areas on several occasions (one to four times) during a span of time (one to five hours) daily at relatively short distances between the points of observations. Therefore, it seems logical to assume that there was a plentiful supply of food in the areas frequented by the armadillos.

Layne and Glover (1977) indicated that there were no overlaps in home ranges of adult females. However, several other authors (Clark, 1951; Fitch et al., 1952; Galbreath, 1982; Breece and Dusi, 1985) reported that overlaps of home ranges of armadillos frequently were conspicuous. We observed numerous instances of overlaps of home ranges between juveniles and adults of both sexes (Table 2). Only one individual (adult male) was determined to not overlap with home ranges of other animals. Overlaps of home ranges and closeness of armadillos frequently observed by us may have been related to pairing behavior of *D. novemcinctus* as discussed by McDonough (1997).

There are relatively few published reports of densities of armadillos. Galbreath (1982) provided an estimated density of these mammals as less than one animal per hectare. Kalmbach (1943) attempted to estimate densities of armadillos based on questionnaire surveys; he reported a high density of 0.82 animals per acre and a low density of 0.21 armadillos per acre. Taylor (1946) gave some estimates of densities of *D. novemcinctus* based on strip counts of active dens. However, he expressed uncertainty with regard to the direct correlation between the numbers of active dens and the numbers of animals occupying the burrows; as many as five armadillos were

found in one den. Taber (1945) attempted to correlate numbers of animals with numbers of dens; he found one armadillo per 4.5 dens as a result of one study and one animal per 8.5 dens in another observation.

Random strip surveys were conducted to estimate the number of armadillos in the study area. A road 1.9 kilometers long, with an adjacent observable, open, grassy area estimated to be 20 acres (8.1 ha), was selected for these surveys. The road was traveled in 10 to 15 minutes and the numbers of armadillos observed were recorded. The results of the strip surveys are depicted in Table 4.

Some seasonal changes were noted in connection with patterns of activities of *D. novemcinctus* in the study area. During the winter and early spring, most of the foraging by armadillos was diurnal. However, as the nights became warmer, the animals began to emerge and forage increasingly later in the afternoons. During the summer, most of the foraging activities of armadillos were nocturnal. Other than periods of inclement weather, such as hurricanes, September and October were the driest periods in the study area. The days were warm and the nights were cool; frequently there were ground fogs and heavy dews in the early evening. Although the ground frequently was dry and cracked, the open, grassy areas were frequented by armadillos during this season. McDonough and Loughry (1997a) reported on

Table 4. Observations of armadillos during strip surveys along 1.9 kilometers of road and adjacent areas of an estimated 20 acres (8.09 ha) in southern Louisiana.

Dates	Times of Observations	Numbers of Armadillos
24 October 1987	1630–1640	14
25 October 1987	1500–1510	10
25 October 1987	1755–1805	8
26 October 1987	1535–1545	4
30 September 1990		42
1 October 1990		41
2 October 1990	1720–1730	29
15 October 1990	1805–1815	51
17 October 1990	1705–1720	60
20 October 1990	1755–1810	54
22 October 1990		18
23 October 1990		16
28 October 1990	1120–1130	18
28 October 1990	1620–1630	31
29 October 1990	1117–1127	7
30 October 1990	1120–1130	17
30 October 1990	1620–1630	29
11 September 1995	1845–1856	6
26 September 1995	1900–1905	5
29 September 1995	1819–1833	8
1 November 1995	1657–1703	10

activity periods of armadillos in northern Florida. They observed considerable flexibility in the timing of activity of these mammals. However, activity was correlated positively with cloud cover during the day and with warm and dry conditions at night.

A summary of patterns of mortality in *D. novemcinctus* was presented by McDonough and Loughry (1997b). They found significantly higher incidences of mortality caused by predators in juveniles as compared to adult armadillos. However, mortality during a prolonged period of drought was greater for adults than for juvenile animals. Armadillos frequently are killed on roads (Loughry and McDonough, 1996). However, reliable estimates of the impacts of road kills on populations are difficult to determine (Case, 1978). As implied previously, mortality of armadillos in the study area was attributed mostly to interactions with humans; a few animals were found dead on roads and some armadillos apparently were shot. Newman (1913) provided information on the slaughter of armadillos for the use of the armor in making baskets. For example, he stated that one dealer claimed to have shipped about 40,000 baskets made from armadillos in a period of six years. Incidentally, ornamental items, such as baskets and purses, as well as stuffed animals, still are available in many markets.

Development.—There have been some conflicting reports in the literature with regard to positions of *D. novemcinctus* during copulation. For example, Newman (1913) and other authors reported that copulation occurred with the female turned on her back. However, Galbreath (1982) observed copulation by the male mounting the female from the back. This position of animals during copulation was correlated with studies of the shape of the penis of the male with the structure of the female urogenital sinus (Newfang, 1947; Galbreath, 1982).

One of us (RDS) observed mounting behavior by armadillos in or near the study area. On 6 September 1984, two armadillos were observed for a considerable period of time. One animal was foraging, and was followed by the other which attempted periodically to mount the foraging animal. Each time the rear animal would try to mount, the foraging armadillo would take a few rapid steps forward, disengage, and begin foraging again. The process was repeated numerous times over a distance of several hundred feet. Although copulation was not observed, the actions of this pair of animals could not be described as aggressive behavior as discussed by Denson (1979) and McDonough (1994). On 25 November 1984, an armadillo was observed mounted on the back of another animal at 2200 hours. Based on the movements of the animals, it was assumed that copulation occurred. Some detailed descriptions of pairing behavior of armadillos were presented by McDonough (1997).

Information on the reproductive cycle of *D. novemcinctus* has been provided by numerous authors. Patterson (1913) reported that old females bred first, mating in most cases before 15 October, while the second-year females continued to breed for some time after this period. He indicated a period of quiescence of about three weeks, with a gestation period of about an additional 140 days, with the majority of young born in March and April. Hamlett (1933) suggested a quiescence period of about 14 weeks in duration. Based on examination of over 2,000 female armadillos killed at intervals throughout the year, Hamlett (1935) reported a total length of gestation of nearly eight months, made up of a "free-vesicle stage" of three and a half

months and an actual development period of about four months. A gestation period of eight to nine months, with an embryonic diapause of three to four months, was suggested by Enders (1966). A comprehensive summary of reproductive strategy in *D. novemcinctus* was presented by Storrs et al. (1989). Although the gestation period of armadillos has been regarded generally as eight to nine months, including a three to four month period of embryonic diapause, captive females not exposed to males gave birth to young 13 to 24 months after capture (Storrs et al., 1989).

Talmage and Buchanan (1954) noted that female armadillos produced new litters as early as February. Lowery (1974) reported that February was typical for time of parturi-tion of armadillos in Louisiana. Enders (1966) found fetuses approaching full-term size usually in late March and early April. During this study, we found the largest fetuses in mid April. However, length of gestation and time of parturition may be influenced by various stresses to which female armadillos are subjected (Storrs et al., 1989).

According to Enders (1966), the time of parturition of armadillos in late March and early April coincided with the presence of large numbers of lactating females. In this study, a non-pregnant female captured on 28 February 1987 weighed 4.0 kg, had nipples 9 mm in length, and a vestibular cleft 10 mm in length. A pregnant female captured on the same day weighed 4.6 kg, had nipples 13 mm in length, and a vestibular cleft 20.5 mm in length. A lactating female captured on 30 April 1986 weighed 4.6 kg and had nipples 20.5 mm in length. Another lactating female captured on the same date weighed 4.5 kg and had similar nipple measurements.

On 21 April 1983, a female, dead-on-road, was examined and prepared as a museum specimen. She weighed 5.0 kg, was not lactating and had not given birth recently. There were unusual amounts of fat everywhere, around the legs, at base of tail and in neck and belly regions.

Illustrations of sets of fetuses of *D. novemcinctus* were provided by Newman and Patterson (1910), Newman (1913), Patterson (1913), and Kalmbach (1943); however, dates when fetuses were obtained and measurements of individuals were not included. Newfang (1947) gave crown-rump measurements of 29 fetuses and the dates that they were preserved. In addition to internal structures, she described and illustrated the external genitalia of armadillos.

The following descriptions of external morphology of fetuses of *D. novemcinctus* are based on sets of fetuses (Table 3). The sets of fetuses are listed in order of average fetus size. Following the date of capture of female are the standard measurements (total length, tail length, hind foot length, and ear length) and weight, when known, of the female (mother). If the individual female had a stub tail, then the total length and tail length measurements are enclosed by parentheses. The seven sets of fetuses, with date of capture and measurements of female are as follows: Set 1, 14 February 1986, (668)-(265)-100-37, unknown weight; Set 2, 28 February 1987, 768-337-96-38, 4.6 kg; Set 3, 11 February 1983, 760-320-70-44, 3.8 kg; Set 4, 15 March 1987, (718)-(302)-96-39, 4.2 kg; Set 5, 10 March 1982, 788-353-91-41, 6.3 kg; Set 6, 15 April 1970, 700-323-95-30, 4.9 kg. Data are reported for an additional set of fetuses obtained on 7 March 1986 (Table 3) from a road-killed female. Measurements for the female were 758-313-100-40, unknown weight. The fetuses were blood-stained and damaged such that accurate measurements could not be obtained for width of the scapular and pelvic

shields. Thus, this set of fetuses was not used in the descriptions of development of external morphology and pigmentation.

Rates of growth of armadillos are depicted in Figure 3. The head, trunk, hind foot, and ear pinnae have a similar pattern of change in relative size during development (Figure 3). The relative proportions of these structures are comparatively stable during the course of early development of the fetuses. However, the tail increases in length at a faster rate than the trunk after a total body length of about 80 mm (Figure 3).

Examples of fetuses from Sets l–6 are shown in Figures 4–6. In the early sets of fetuses (Sets 1–4), there was little color (Figure 4). In some cases, the internal organs could be seen through the translucent skin of the belly and the band region of the carapace. In fetus Set 5, adult coloration was discernable and the areas between the scutes were pigmented. However, pigmentation was most obvious on the posterior part of the head, the pinnae, the dorsal part of the carapace, and the bases of the hind feet (Figure 5). The fetuses of the Set 6 essentially were of the same coloration as the adults; but the fetuses were lighter brown in color than the adults (Figure 6).

Progression of the development of the heads was obvious in the sets of fetuses that we examined. In the 1st set of fetuses, the eyes were developed, the lenses could be discerned, and the eye lids were open partially. In fetus Set 2, the eye lids were fused together, but the lenses were obvious. However, in fetuses of Set 3, the eye lids were thicker and opaque; the lenses were obscured. In fetus Set 5, there were narrow slits between the eye lids. In fetuses of Set 6, the eyes were half open.

The nostrils appeared as small pits in the first set of fetuses studied. During subsequent development, the pits were increasingly deeper and greater in diameter. In fetus Set 4, fleshy folds were present that divided the holes vertically and made them appear more slit like. These structures were increased in size in the remaining sets of fetuses.

In the fetus Set 1, the tips of the pinnae were folded inward to close the openings in the ears; the bases of the pinnae were not adhered to the head. However, in fetus Set 2, the bases of the pinnae were adhered to the head, but the tips were not folded inward. These positions of the pinnae were present in all of the other sets of fetuses. In fetus Set 4, development of scutes was noted at the bases of the pinnae. Approximately half of the pinnae were covered with scutes in fetus Set 5. In fetus Set 6, the pinnae were equipped fully with scutes. The distances between the right and left pinnae were similar in all of the fetuses examined. It seemed that the head increased in width and the pinnae enlarged, thus creating the perception that the ears became closer together and moved from the sides to the tops of the heads of the developing fetuses.

The tongues were protruding conspicuously from the mouths of all fetuses of Set1 and Set 2. In fetus Set 3, the tongues were enclosed completely within the mouths of the animals. Perhaps the rates of growth of the jaws exceed those of the tongues. In the smallest fetuses (Sets l–3), the tongues were round in cross section; in Sets 4–6, the tongues were flattened in cross section.

In the smallest fetuses, the jaws were flattened and without well-defined edges. However, the edges of jaws were outlined in the fetuses of Set 2, and well developed in Set 5 and Set 6. All fetuses examined lacked teeth. In fetus Sets 1 and 2, the lower

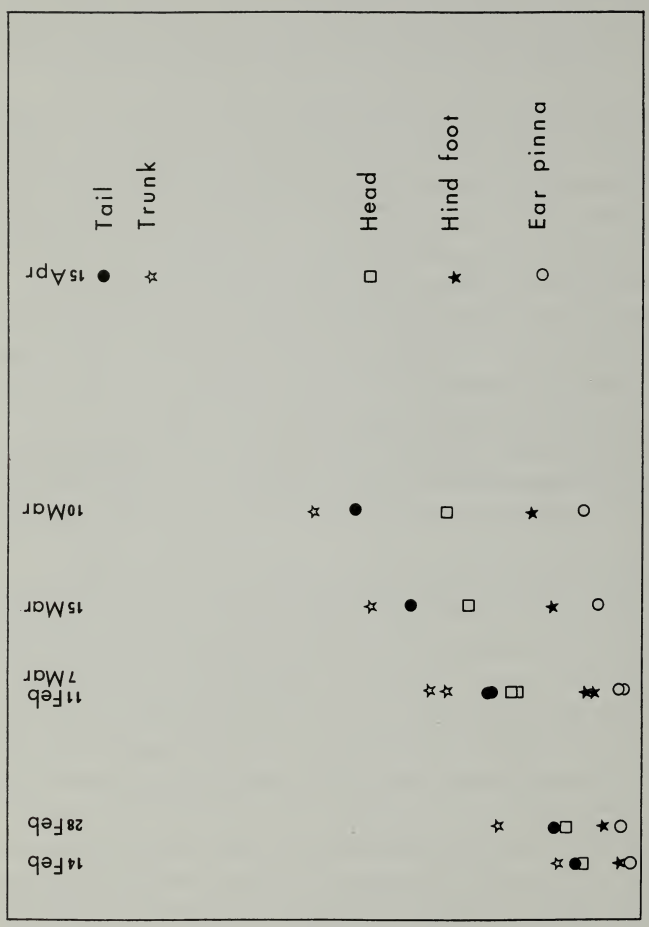

Figure 3. Relative growth of tail, trunk, head, hind foot, and ear pinnae of six sets of fetuses of armadillos from southern Louisiana. Symbols represent the mean value of the respective embryos.

Figure 4. Photographs of representatives from fetus Set 1, Set 2 and Set 3 of armadillos from southern Louisiana.

Figure 5. Photographs of representatives from fetus Set 4 and Set 5 of armadillos from southern Louisiana.

and upper jaws were of the same length. In subsequent sets of fetuses, the upper jaws were more and more protruding; most of the increases in the lengths of the heads were due to the growth of the upper jaws. In fetus Set 6, the upper jaws were 8 mm longer than the lower jaws. Incidentally, this was when fleshy lips were first detected on the fetuses studied.

In fetus Set 1, sutures of the underlying bones of the cranium were visible. In fetuses of Set 2, primordials of scutes were noticeable on the posterior ends and the

Figure 6. Photograph of representative from fetus Set 6 of armadillos from southern Louisiana.

central parts of the tops of the heads. In the remaining fetuses, the individual scutes were distinguishable; the head shields were well defined on the posterior parts of the head (by a skin fold) and also on the snouts of the fetuses. On the snout of each fetus, the shields were interrupted by a single line extending from the edges of the eyes anteriorly to the tip of the snout.

There was noticeable progression of the development of the trunks in each of the sets of fetuses studied. The trunks became changed from arched shapes to extended ones; this trend was conspicuous as demonstrated by examination of the six sets of fetuses (Figures 4–6). The areas that would be eventually covered by the carapaces were already well defined in the smallest fetuses. All nine bands already were present in the dorsal regions, and the anlages of the first five rows of scutes could be discerned. The edges of the carapaces already slightly overlapped the venters and upper extremities of the limbs. In fetus Set 2, the anlages of all scutes were distinguishable from each other. The anlages of the scutes started as small, white spots, but soon became enlarged until the different scutes almost were touching each other. In subsequent sets of fetuses, the individual bands were increasingly longer. The different shapes of the scutes (elongate-triangular in the bands, octagonal on the pelvic shields) were established first in fetus Set 4.

In fetus Set 1, genital papillae were present. The umbilical cords were situated short distances anterior to the papillae. In fetus Set 2, whitish blotches were arranged in rows on the venters of the animals. However, by fetus Set 5, the whitish blotches were in irregular patterns. These white spots may be the anlages for the dermal nuclei that become the sites for hair tufts in adult armadillos. The spots

initially were located on the bellies of the animals, but later (fetus Set 4) were noticeable on the chins, throats, and the upper parts of the legs. No hairs were noticed on the fetuses examined. The anal aperatures were apparent first in fetus Set 5. In fetuses of Set 6, the anal aperatures were slit-like at the crests of slight elevations. In fetus Set 6, nipples were visible.

In the smallest fetuses (Set 1), the tails were curled anteriorly between the hind legs. In fetus Set 2, the tails were uncurled partially; development of bony rings on the tails was detected. The anlages of seven different rings were distinguished; the tails became separated from the carapaces by folds of skin. In fetus Sets 3 and 4, anlages for eight rings were present, and different scutes became distinguishable in the 4th set of fetuses. In fetuses of Set 5, 13 different rows could be counted; in the anterior ten rows, each of the rings consisted of two rows of scales which is the pattern present in adult armadillos.

Initially, the development of the forefeet seemed more rapid than that of the hind feet. In fetuses of Set 1, the four digits of the forefeet were well separated, with some webbing at the bases of the digits. The middle digits were the largest, and the anlages for the claws were present. In fetus Set 2, the webbing was absent and the anlages for the claws had ventral grooves. In fetuses of Set 3, toe-pad like enlargements of the claws were apparent, and the anlages for the scutes (in rows) became obvious. The two middle toes were considerably larger than the first digits. In fetuses of Set 5, the individual scutes were distinguishable; the scutes were partially overlapping. The pad-like structures at the tips of the digits were diminished in relative size; the bases of the claws showed some pigmentation. In fetus Set 6, the claws almost were completely pigmented. The development of the hind feet followed about the same patterns as that of the forefeet. However, in the first four sets of fetuses, the development of the hind feet was less rapid than that of the forefeet. In addition, five digits were present on the hind feet; the third toe was decidedly the largest. In fetus Set 4, anlages of scutes were present on the undersides of the hind feet; fetuses of Set 5 had fewer scute anlages.

Acknowledgments

We extend our sincere gratitude to Rudolph Meier, who did a preliminary analysis of part of the home range data and for his excellent descriptions of six of the seven sets of fetuses. Also, we wish to thank the following individuals for their help with the field work associated with the study of home range: Frances Miller Cashner, Robert C. Cashner, Anthony Laska, Kaneta Lott, Jayson S. Suttkus, Ramona L. Suttkus, Frank I. Thomas, and Bruce A. Thompson. Lastly, we thank Craig Hood and an anonymous reviewer for their critical review of the manuscript.

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SYSTEMATIC REVIEW OF SUBGENUS *FUSCATELUM* OF *ETHEOSTOMA* WITH DESCRIPTION OF A NEW SPECIES FROM THE UPPER BLACK WARRIOR RIVER SYSTEM, ALABAMA

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Abstract

The subgenus *Fuscatelum* was thought to contain a single, widespread, lowland species, the goldstripe darter, *Etheostoma parvipinne*. However, comparison of populations from throughout the goldstripe darter's reported range has revealed that populations in the upper Black Warrior River system represent a new species. The new species has lower scales counts than the goldstripe darter, lacks the distinctive gold stripe, and has a less intensive pattern of brown pigmentation along its sides. There are concerns about the conservation status of the new species, because only three rather widely separated populations are known, and the species cannot be reliably taken in any of these areas. In addition to describing the new species, we redescribe the goldstripe darter and review morphological attributes of subgenus *Fuscatelum*.

Introduction

The goldstripe darter, *Etheostoma parvipinne* Gilbert and Swain, inhabits small, vegetated Coastal Plain streams across a broad area of the Gulf and extreme lower Atlantic slopes. Maps of the distribution of this species show the species occurring well above the Fall Line only in the Black Warrior River system in Alabama (Rohde, 1980; Page, 1983, Figure 1). Careful study of these populations has revealed that they represent a distinct species.

In this paper we describe the new species, redescribe *E. parvipinne* based on material from throughout its geographic range, and review morphological attributes and systematics of subgenus *Fuscatelum*.

Materials and Methods

Material used in this study was obtained from fish collections at Auburn University (AUM), Geological Survey of Alabama (GSA), Southern Illinois University (SIU), Tulane University Museum of Natural History (TU), University of Alabama (UAIC), and the University of Texas Memorial Museum (TNHC). Paratypes of the new species were deposited at Academy of Natural Sciences, Philadelphia (ANSP), Illinois Natural History Survey (INHS), University of Alabama, University of Florida

Tulane Studies in Zoology and Botany 31: 23–50. 1999.

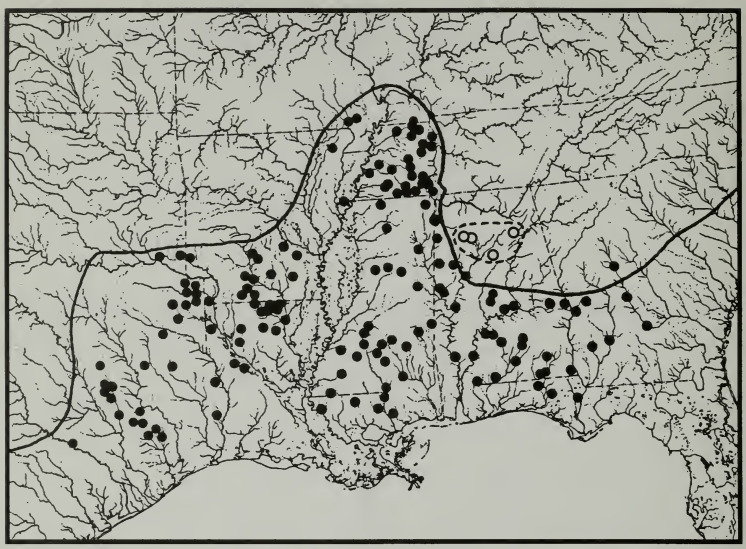

Figure 1. Map of the distribution of darters in subgenus *Fuscatelum* in relation to the Fall Line (heavy line). Open circles within dashed line represents known populations of *E. phytophilum* in the upper Black Warrior River system of Alabama. Solid circles mostly below the Fall Line show the distribution of *E. parvipinne*. (Map modified from Richards, 1963).

(UF), University of Michigan (UMMZ), and the United States National Museum of Natural History (USNM).

Counts and measurements follow Hubbs and Lagler (1958) except that transverse body scales were counted from the origin of the anal fin diagonally upward to the base of the spinous dorsal fin, and only branched rays in the caudal fin were counted. The great range in variation of lateral-line and pored lateral-line scale counts made it difficult to format the tables to fit on a page. Data for these counts are reported in two-scale intervals simply to reduce the width of Tables 1 and 2. Thus, counts of 38 and 39 in Table 1 are tabulated under "38–39", and so on. Vertebral counts were made from radiographs of 20 specimens from a Tombigbee River system population of *E. parvipinne* (TU 76977), and 27 specimens from the Turkey Creek (AUM 27017) and Clear Creek (TU 162757) populations of the new species.

Data for 15 body measurements, including standard length (SL), were gathered for samples of 17 males and 13 females from the lower Black Warrior population of *Etheostoma parvipinne* (GSA 6848.06, GSA 6855.06, GSA 7204.09, GSA 7249.08, GSA 7384.11, GSA 7993.11 and TU 168007, all Tuscaloosa Co., AL) and 15 males and 15 females from Turkey and Clear Creek populations of *E. phytophilum* (AUM 18747,

AUM 21148, AUM 21155, AUM 27017, TU 163757, TU 176230 and Holotype, TU 187503). Measurements were made with needle point calipers to the nearest 0.1 mm. Data for 14 of the body measurements were converted to ratios of standard length. The ratios were arcsine transformed to normalize ratio distributions. The transformed ratios were subjected to ANOVA to test for differences between sexes within species, and between species within each sex.

The arcsine-transformed mensural data were also subjected to principal components analysis (PCA) to characterize shape differences between the two species. PCA was performed on the covariance matrix because the data were not standardized. All statistical analyses were performed on a personal computer with Microsoft Excel 97 and Statistical Analysis System (SAS) Inc., software. Names used for species associates of the new species follow Robins et al. (1991).

Subgenus ***Fuscatelum***, Page, 1981

Type Species: *Etheostoma parvipinne* Gilbert and Swain (in Gilbert, 1887).

Diagnosis: Subgenus *Fuscatelum*, as diagnosed by Page (1981), is distinguished by the absence of bright breeding colors (red, blue, green or yellow) on body or fins, presence of a frenum, and presence of tubercles on the anal fin of breeding males (Page, 1981). As pointed out by Shaw (1996), the combination of these characters distinguishes *E. parvipinne* from all other *Etheostoma* except *E. fusiforme*. The addition of caudal peduncle depth/SL ratio greater than 0.11 (vs. less than 0.11 in *E. fusiforme*) distinguishes *Fuscatelum* from all *Etheostoma* inclusive of *E. fusiforme*.

Description: The following is a summary of the morphological characteristics of subgenus *Fuscatelum*, based on the new species and all populations of *E. parvipinne* examined in this study. For completeness, some of this description is repeated in the species accounts below.

Lateral line is straight and nearly (91–98%) complete. The nape, cheek, opercle, prepectoral area, breast and anterior belly are fully scaled (cheek scales sometimes partially embedded). A broad premaxillary frenum is always present. Branchiostegal membrane is moderately to broadly connected across the isthmus.

The head is brown dorsally with an even darker brown horizontal stripe running on either side from top of opercle through eye, across snout and onto upper jaw. A thick dark brown subocular bar extends down onto underside of the head. Side and underside of head below lateral stripe light yellow-brown to whitish-yellow with only a scattering of melanophores. Lower jaw and chin also light yellow-brown to whitish-yellow with darker brown edging or flecking. Opercle brown; humeral spot weakly developed. Brown pigment on body diffuse, giving the sides a more or less continuous brown cast, or producing a dense mottling of brown that dissipates dorsally and ventrally. When most intense, the brown pigment forms a series of 8–10 irregular dashes or blotches along the side of body, which may be extended into a series of vertical bars. Dorsum darker than ventrum but lighter than sides.

Medial fins have dark brown pigment forming a varying number of wavy bands. The bands are most numerous on the caudal fin and least developed on the anal fin.

Most of the pigment forming the bands is along the edges of fin rays. Fin membranes adjacent to the bands have only a scattering of melanophores, making the bands appear interrupted. The base of the caudal fin has two to four dark brown spots of varying intensity. Paired fins lack pigment in non-breeding individuals.

Breeding males differ from the above pattern mainly in having black melanophores scattered over all of the body and fins (least so on the pectoral), giving the body a dusky cast. Black pigment is concentrated on the anterior interradial membrane of the spinous dorsal fin in mature males, producing a distinct blotch. The rest of the first dorsal fin is dusky except for a white (pigmentless) strip along the distal margin. The soft dorsal, anal, pelvic and (less so) pectoral fins also develop black melanophores on the interradial membranes, making the fins appear dusky. Breeding tubercles develop only on anal soft rays of nuptial males. Female genital papillae are bulbous at the base and extended into a tube distally. Papillae of males very short and tubular, though wider at base than at tip.

As mentioned above, the caudal peduncle in subgenus *Fuscatelum* is relatively deep (more than 0.118 when expressed as a proportion of standard length), most like the situation in subgenera *Catonotus* and *Nothonotus* (Page 1981, Brooks 1993). The snout is very short (0.054–0.58 of standard length for both *E. parvipinne* and *E. phytophilum*). In this regard, subgenus *Fuscatelum* is most like subgenus *Boleichthys* (*sensu* Page, 1981). Pectoral fin length (0.205–0.224 of standard length) and soft dorsal fin base length (0.14 of standard length) are short relative to other *Etheostoma* (Page, 1981; Brooks, 1993). In this regard subgenus *Fuscatelum* is most like *E. exile* (subgenus *Boleichthys*, *sensu* Page, 1981; subgenus *Oligocephalus*, *sensu* Bailey and Etnier, 1988). Finally, the caudal fin is relatively long (0.212–0.229 of standard length), similar to the condition in subgenera *Boleichthys*, *Boleosoma*, *Catonotus*, *Psychromaster*, *Villora*, and *Ozarka*.

Systematics: *Etheostoma parvipinne* has been traditionally allied to darters in subgenus *Oligocephalus*. Richards (1963) concluded that *E. parvipinne* formed a natural group with *E. fricksium* and *E. mariae*, then also classified in subgenus *Oligocephalus*. Richards (1963) speculated that *E. parvipinne* was derived from an *E. fricksium*-like prototype through advancements such as reduction in dorsal fin color and interruption of the supratemporal canal. Page (1981) removed *E. parvipinne* from subgenus *Oligocephalus*, and established for it the subgenus *Fuscatelum* to emphasize its lack of bright breeding colors. Page (1981) considered *Fuscatelum* to be part of a highly evolved group of darters, which included members of the subgenera *Nothonotus*, *Belophlox* (*E. fricksium* and *E. mariae*), *Ozarka* (*E. punctulatum* and allies), *Oligocephalus*, *Catonotus*, and perhaps *Villora* (*E. edwini*). Bailey and Etnier (1988) commented that *Fuscatelum* shares a number of traits with subgenus *Ozarka*, including tuberculate anal fin, a distinctively depigmented nape, and late winter habits which suggested reproduction in "temporarily flooded fields" as seen in subgenus *Ozarka*.

No consistent hypothesis of relationships has emerged from three phylogenetic analyses involving subgenus *Fuscatelum* (Shaw, 1996; Wood and Mayden, 1997; Turner, 1997). Shaw (1996) analyzed 141 osteological, external morphological, and behavioral characters for 82 species of darters (genera *Crystallaria*, *Ammocrypta*, *Percina*, *Etheostoma*) and three Eurasian percids. In this analysis, *Fuscatelum* (*E. parvipinne*)

was sister to all other *Etheostoma* (76 species representing all traditionally allied subgenera, except *Ioa*), suggesting that *Fuscatelum* is the most ancestral subgenus in genus *Etheostoma*.

Wood and Mayden (1997) analyzed allozyme variation at 32 presumptive gene loci for 26 species of darters (genera *Crystallaria*, *Ammocrypta*, *Percina*, and *Etheostoma*) and three other percids. The most parsimonious solution was a tree based on allozyme frequencies with a topological constraint among outgroups consistent with previously published work. Subgenus *Fuscatelum* (*E. parvipinne*) occupied a more derived position in this phylogeny than in the analysis by Shaw (1996), and was sister to a group consisting of *Ozarka* (*E. cragini*)+ *Catonotus* (*E. flabellare* + *E. crossopterum*). This group was sister in turn to subgenus *Boleichthys* (*E. gracile* + *E. microperca*). Subgenus *Belophlox* was not represented in the analysis.

Turner (1997) analyzed sequence data from the mitochondrial DNA control region. Again, subgenus *Fuscatelum* (*E. parvipinne*) was more derived than in the analysis by Shaw (1996). It was most closely related to subgenus *Villora* in the most parsimonious topology, and was in a group of darters—together with representatives of the subgenera *Belophlox* (*E. mariae*), *Boleichthys* (*E. exile*, *E. gracile*), *Ozarka* (*E. pallididorsum*), *Villora* (*E. edwini*), and *Oligocephalus* (in part)—which lacked a tandem repeat at the proline tRNA end of the control region.

Fuscatelum shares a depigmented lateral line and a similar pattern of blotches or dashes along the side (most like *E. mariae* in this regard) with darters in subgenus *Belophlox* (Richards, 1963). The spinous dorsal fin of breeding males of *E. parvipinne* and *E. phytophilum* has a clear to milky-white marginal band with black pigment concentrated in the anterior interradial membranes, a situation most like that seen in *E. mariae* of subgenus *Belophlox* (Richards, 1963) and in some *Nothonotus*, but without the other band(s) of color seen in the spinous dorsal fin in these groups. Shaw (1996) mistakenly coded the spinous dorsal fin marginal band color as black in *Fuscatelum* (state 3), rather than opaque/tan/milky-yellow (state 4), as interpreted for *E. mariae*, members of *Nothonotus* and *E. blennioides*. She attributed character state 0 (marginal band clear) to *E. fricksium*, when in fact the margin of the spinous dorsal in breeding males of this species is clear to opaque-white with a stippling of black melanophores.

Etheostoma phytophilum, new species
Rush Darter
Figure 2a, b

Etheostoma parvipinne. Mettee 1978:144 (account, Fishes of the Birmingham-Jefferson County region of Alabama with ecological and taxonomic notes); Rohde 1980:680 (distribution, in part); Page 1983:245 (distribution, in part); Kuehne and Barbour 1983:141 (distribution, in part); Mettee et al. 1989a:181 (distribution, in part); Mettee et al. 1989b:144 (distribution, in part—Atlas); Page and Burr 1991:413 (distribution, in part—Map 359); Mettee et al. 1996:654–655 (distribution, in part, reference to distinct form in Turkey Creek system, Jefferson Co.).

HOLOTYPE: TU 187503: Spring run trib. to trib. to Turkey Creek along Alabama

Highway 79, Pinson, Jefferson Co, AL, 1 April 1994, H. Bart, J. Buckley and C. Gradney, collectors.

PARATOPOTYPES: TU 176230 (3, collected with holotype); AUM 18747 (1), 11 March 1979; AUM 21155 (2), 8 July 1979; AUM 27017 (17, distributed as follows: AUM 27017 (5), ANSP 177501 (2), INHS 48900 (2), UAIC 1295.01 (2), UF 110739 (2), UMMZ 234787 (2), USNM 351328 (2)) 6 November 1990; UAIC 11064.01(2), 17 April 1994.

OTHER PARATYPES: AUM 21148 (1): AL, Jefferson Co., Penny's Spring, 8 July 1979; TU 60078 (1): AL, Jefferson Co., Turkey Creek , 20 October 1969.

ADDITIONAL MATERIAL EXAMINED, NOT DESIGNATED AS TYPES: Wildcat Branch, trib. to Clear Creek, Winston Co., AL: AUM 27031 (11), 27 November 1990; TU 162757 (10), 11 April 1992; TU 167887 (2), 26 February 1993; TU 167895 (3), 27 February 1993; UAIC 10645.01 (in part 16), 25 February 1993; Cove Spring, Etowah Co., AL: UAIC 4139.04 (1), 4 May 1975.

DIAGNOSIS: *Etheostoma phytophilum* is a member of subgenus *Fuscatelum* as diagnosed herein and by Page (1981). It differs from the only other species in the subgenus, *E. parvipinne*, in usually having 47 or fewer lateral line scales (lateral line scales usually 48 or higher in *E. parvipinne*), usually 13 or fewer transverse scales (tranverse scales usually 14 or higher in *E. parvipinne*), and 22 or fewer caudal peduncle circumferential scales (caudal penduncle scales usually 23 or higher in *E. parvipinne*). Lateral line not distinctly depigmented at any stage (lateral line distinctly depigmented, especially anteriorly, in female and non-breeding *E. parvipinne*).

DESCRIPTION: *Etheostoma phytophilum* is a moderate-sized species of *Etheostoma*: the average size of the 68 specimens examined in this study (none less than 30 mm SL) is 40.22 mm SL; the largest known specimen is a 58 mm SL female. Lateral line with 39–51 scales (usually 47 or fewer) of which 32–50 are pored (Tables 1 and 2). Transverse scales 10–14, (usually 13 or fewer, Table 3). Caudal peduncle circumferential scales 18–22, usually 21 (Table 4). Only 10 of 68 *E. phytophilum* examined (15%) had more than 47 lateral line scales, only 2 of 68 (3%) had more than13 transverse scales, and none had more than 22 caudal peduncle scales. The combination of lateral line scales 47 or fewer, transverse scales 13 or fewer, and caudal peduncle scales fewer than 22, was seen in only 25 of 376 specimens (6.7%) of *E. parvipinne* examined from through the species' geographic range.

First dorsal fin has 8 to 11 (usually 10) spines and is entirely separate from the second dorsal fin, which has 9–13 (usually 10–11) soft rays (Tables 5 and 6). The right side pectoral fin has 14–16 (usually 15) rays (Table 7). The pelvic fin always has one spine and six rays. The anal fin almost always has two spines (although one may be reduced) and 7 to 10 (usually 9) soft rays (Table 8). The caudal fin has 11–15 (usually 13) branched rays (13–15 principal rays, Table 9). Vertebrae number 35–37 ($\bar{x}$ = 36.4).

Cephalic lateralis system is as follows: lateral canal complete with 5 pores, supratemporal canal incomplete with two pores; supraorbital canal complete with four pores; a coronal pore is usually present; infraorbital canal complete with 5–10 (usu-

Figure 2. a) *Etheostoma phytophilum*, holotype (TU 187503), breeding male, 44 mm SL, spring run in the Turkey Creek system; b) *E. phytophilum*, breeding male, 43 mm SL, Wildcat Branch trib to Clear Creek (TU 167895).

ally 8) pores (Table 10); preoperculomandibular canal complete with 9–12 (usually 10) pores (Table 11).

Color in life khaki (light yellowish brown) to golden brown, with a pattern of darker gray-brown pigment overlaying a yellowish to golden ground color. Head gray-brown dorsally with a dark brown stripe running horizontally from top of opercle, through eye, across snout, and onto upper jaw. A dark brown vertical bar runs below eye to underside of the head. Brown pigment on body diffuse, giving the sides a brown cast or producing a dense mottling of brown that dissipates dorsally and ventrally. At its most intense, the brown pigment forms a series of 8–10 irregular dashes along the side of body. Dorsum darker than ventrum but lighter than sides.

Even at its most intense, the brown pigment on the sides of the rush darter is seldom as intense as in the goldstripe darter, and mid lateral dashes are never drawn into vertical bars, as frequently seen in breeding males of *E. parvipinne*. The distinct gold stripe typical of *E. parvipinne* is never well developed in *E. phytophilum*. Only a very narrow strip may be depigmented along the anterior portion of the lateral line, above the midlateral dashes.

Brown pigment occurs at intervals along the edges of fin rays in median fins, producing a varying number of wavy bands. Fin membranes adjacent to the bands have a scattering of melanophores that make the bands appear interrupted. The base

of the caudal fin has two to four dark brown spots of varying intensity. Paired fins lack pigment in non-breeding individuals.

Breeding males of *E. phytophilum* have black melanophores scattered over all of the body and fins (least so on the pectoral fin), making the body appear dusky. A concentration of black melanophores forms on anterior interradial membranes of the spinous dorsal fin in mature males, producing a distinct blotch. The rest of the first dorsal fin is dusky except for a white (pigmentless) strip along the distal margin. The soft dorsal, anal, pelvic and (less so) pectoral fins also develop a dusky appearance due to the presence of black melanophores on interradial membranes. Breeding tubercles develop only on anal soft rays of nuptial males, female genital papillae are bulbous at the base and extended into a tube distally, and genital papillae of males are short and tubular, though wider at base than at tip.

Variation: The population in the Clear Creek system has slightly higher average counts of lateral line and pored lateral line scales than the Turkey Creek population. The Clear Creek population also has higher modal counts of right pectoral (16) and branched caudal fin rays (14) than the Turkey Creek population (modes of 14 or 15, and 13, respectively). Dorsal soft rays are modally lower in the Clear Creek population (10) than in the Turkey Creek population (11 or 12). None of the differences is statistically significant. In the Clear Creek system population, breeding males tend to have more mottling on the lower sides than in males from the Turkey Creek population. Clear Creek breeding males also develop a yellowish cast in the spinous and soft dorsal, pectoral and caudal fins (Figure 2b). We collected only two males in high reproductive stage in the Turkey Creek system (the holotype and a paratype form the same collection), and neither of them had yellow pigment in the fins. An older March-collected specimen was too faded to discern fin coloration. The Cove Creek population cannot be adequately compared because it is represented by a single specimen.

Distribution: *Etheostoma phytophilum* is endemic to upland portions (Appalachian Plateau and Valley and Ridge provinces) of the Black Warrior River system in Alabama. Only three rather widely separated populations are known (Figures 1 and 3): one in streams in the Clear Creek system, a tributary of the Sipsey Fork of the Black Warrior River in Bankhead National Forest; one in springs tributary to Turkey Creek north of Birmingham, AL; and one in a spring around Little Cove Creek near Gadsden, AL (a single specimen known from this location). The latter two streams are tributary to the Locust Fork of the Black Warrior River. Considering the area of the upper Black Warrior River system over which *E. phytophilum* occurs (Figure 3), and the large number of springs in this area, it would seem likely that other populations exist. The sampling locations depicted in Figure 3 give the impression that the upper Black Warrior Basin has been extensively sampled. However, the vast majority of the sampling locations are on streams larger than those that support *E. phytophilum*. Small streams and spring runs in the upper Black Warrior system need to be surveyed to determine the full extent of the rush darter's distribution.

Habitat and Biology: *Etheostoma phytophilum* is an uncommon species that is

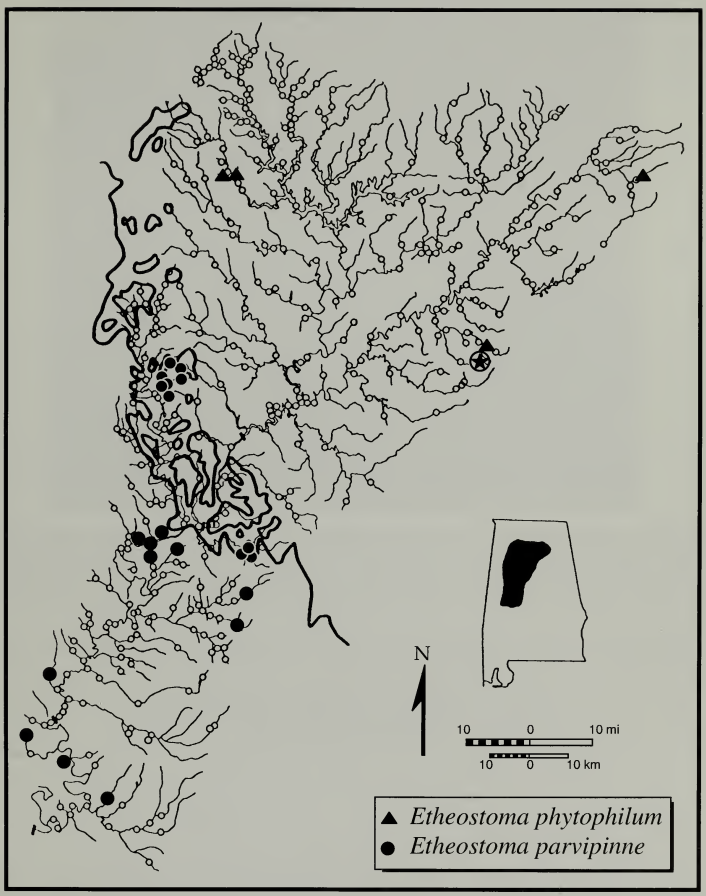

Figure 3. Map of the Black Warrior River system in Alabama, showing collection sites (open circles) and the distributions of *Etheostoma parvipinne* (solid circles), *E. phytophilum* (solid triangles, with circled star representing the type locality) in relation to the Fall Line (heavy broken line). Map modified from Mette et al. (1989a).

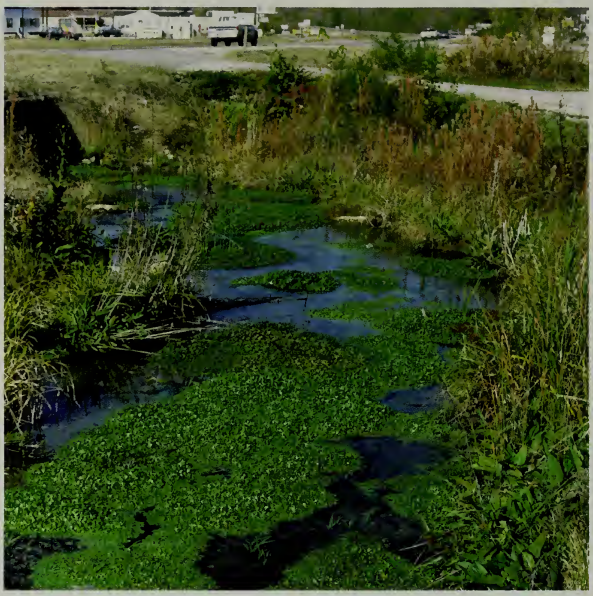

Figure 4. Type locality of *Etheostoma phytophilum*, showing the proximity to Alabama Highway 79. Note the abundant stream-side vegetation (prefered habitat of the rush darter) and the evidence of spring influence (watercress in mid channel).

usually taken in low numbers (fewer than 10 specimens). We have had the most success collecting the species from the root masses of emergent vegetation in very shallow water along the margin of small spring-fed streams (Figure 4). Vegetation types include rushes (*Juncus* spp.), dock (*Rumex* spp.), and a variety of unidentified grasses (Gramineae). Although water along the margins of these streams is shallow, it is typically clear, cool and flowing. The rush darter is never taken in the thick growths of water cress found both along the sides and at mid-channel in spring runs in the Turkey Creek system. The two streams in the Clear Creek system (Sipsey Fork of the Black Warrior) where rush darters have been collected appear to be less spring-influenced than streams in the Locust Fork, and the streamside vegetation is thick, tall and dominated by rushes and grasses. Cove Spring in Etowah Co., AL, where a single rush darter was collected, flows into a reach of Cove Creek which is impounded by beaver. Lower reaches of Cove Spring Run appear to offer good habitat, but are difficult to access and sample effectively.

Males taken in March and April are tuberculate and exhibit dusky breeding pigmentation. Females collected in March and early April have enlarged ovaries

with large ripening oocytes. Spawning and other aspects of life history are presently unknown.

In the Turkey Creek system, species associates of the rush darter include *Campostoma oligolepis*, *Cyprinella callistia*, *Luxilus chrysocephalus*, *Semotilus atromaculatus*, *Lepomis cyanellus*, *Etheostoma whipplei artesiae* and *Cottus carolinae*. In the Clear Creek system, species associates include *Ichthyomyzon gagei*, *Campostoma oligolepis*, *Luxilus chrysocephalus*, *Nocomis leptocephalus*, *Notropis baileyi*, *Semotilus thoreauianus*, *Erimyzon oblongus*, *Lepomis cyanellus*, and *Percina nigrofasciata*.

Concerns about the conservation status of *E. phytophilum* are increasing because of its sporadic occurrence in streams in the Clear Creek and Turkey Creek systems, increasing threats to habitat quality in the latter, and our inability to collect the species in Cove Spring. The species is known from three locations in the Turkey Creek system, but cannot be reliably collected at any of these locations. The type locality is a spring run that forms part of the road side drainage system along Alabama Highway 79, southwest of Pinson, AL. The stream has been modified extensively and receives runoff from several business. Mainly because of the spring influence, upper reaches of the spring run continue to offer what appears to be favorable habitat. Specimens of *E. phytophilum* have also been taken in a spring north of Pinson on two occasions (a total of two specimens, only one of which is archived). The watercress darter *E. nuchale* was introduced into this spring by W. Mike Howell in 1988 to reduce a then looming threat of extinction of this species due to destruction of its native habitat (Mettee et al., 1989a). The watercress darter appears to be doing well in the spring; the rush darter is rare.

Etymology: The name *phytophilum* is derived from the Greek words phytum, meaning plant or vegetation, and philo meaning to love or loving, and is in reference to the preference of this species for emergent vegetation along stream margins. The vernacular name, rush darter, is suggested because rushes (*Juncus* spp.) are an obvious component of the stream side vegetation in streams inhabited by *E. phytophilum*.

Etheostoma parvipinne Gilbert and Swain
Goldstripe Darter

Etheostoma (*Etheostoma*) *parvipinne* Gilbert and Swain in Gilbert, 1887:59–60 (original description).

Etheostoma squamiceps Bollman, 1886:464–465; Escambia River at Flomaton. Gilbert, 1891:156,159 (Alabama records: Little Escambia River; 1 mile south of Pollard; Sandy Creek, 3 miles east of Evergreen), and Escambia River system. Jordan and Evermann, 1896: 1096 (in part, incorrectly synonymized *E. parvipinne* in *E. squamiceps*).

Claricola squamiceps Jordan et al., 1930: 292 (in part, incorrectly synonymized *E. parvipinne* in *C. squamiceps*).

Poecilichthys parvipinnis. Hubbs and Black, 1941: 9 (validation, not a synonym of *P. squamiceps*). Moore and Cross, 1950: 145–146 (confirmation of Hubbs and Black's, 1941 validation; comparison with *P. squamiceps*; characters; distribution). Moore and Rigny, 1952: 7.

HOLOTYPE: USNM 36716, male 43.0 mm SL, small spring branch tributary to the Black Warrior at Tuscaloosa, AL, summer 1884, C.H. Gilbert and J. Swain, collectors.

MATERIAL EXAMINED:Colorado River Dr.: TNHC 23901 (6): TX, Bastrop Co., Alum Creek; TNHC uncataloged (8): TX, Bastrop Co., Alum Creek. Brazos River Dr.: TNHC 11436 (1): TX, Leon Co., Long Hollow Creek. San Jacinto River Dr.: TNHC 1205 (13): TX, Montgomery Co., Trib. to Peach Creek; TNHC 1346 (1): TX, Polk Co., Trib. to Trinity River; TNHC 2614 (1): TX, Polk Co., Morgan Creek; TNHC 2722 (1): TX, Polk Co., Bluff Creek; TNHC 2749 (13): TX, Walker Co., Gum Branch; TU 74010 (1): TX, Montgomery Co., Stewart Creek. Sabine River Dr.: TNHC 1523 (1): TX, Smith Co., Trib. to Harris Creek; TNHC 2455 (1): TX, Anderson Co., Copperas Creek; TU 60256 (3): LA, Beauregard Par., Hoosier Creek; TU 86888 (1): TX, Newton Co., Big Cow Creek; TU 86935 (2): LA, Beauregard Par., Anacoco River; TU 103251 (5): TX, Tyler Co., Drakes Branch. Red River Dr.: TNHC 2454 (3): TX, Morris Co., Boggy Creek; TNHC 3654 (8): TX, Upshur Co., Trib. to Big Cypress Bayou; TNHC 3928 (11): TX, Bowie Co., Caney Creek; TNHC 12381 (1): TX, Upshur Co., Jones Creek. Obion River Dr.: SIU 3335 (16): TN, Weakley Co., Old Knob Creek; SIU 4126 (14): TN, Weakley Co., Old Knob Creek. Tennessee River Dr.: TU 87968 (1): MS, Alcorn Co., Sevenmile Creek; TU 88014 (5): MS, Tishomingo Co., Little Yellow Creek; TU 88580 (7): MS, Tishomingo Co., Little Yellow Creek; TU 88656 (1): MS, Tishomingo Co., Caney Creek; TU 88666 (4): TN, McNairy Co., Trib. to Tennessee River; TU 88689 (1): TN, McNairy Co., Owl Creek; TU 89326 (1): TN, Hardeman Co., Hatchie River; TU 153375 (2): MS, Tippah Co., Hatchie River. Lower Mississippi River: TU 33049 (2): MS, Lafayette Co., Trib. to Yacona River; TU 55713 (1): MS, Jefferson Co., North Fork Coles Creek; TU 56552 (1): MS, Wilkinson Co., Little Buffalo Creek; TU 57952 (1): MS, Wilkinson Co., Little Buffalo River; TU 61654 (4): MS, Wilkinson Co., Buffalo Bayou; TU 64850 (2): MS, Copiah Co., Bayou Pierre; TU 67983 (8): MS, Lincoln Co., Homochitto River; TU 68014 (2): MS, Lincoln Co., Homochitto River; TU 68060 (1): MS, Lincoln Co., Homochitto River; TU 69003 (1): LA, West Feliciana Par., Thompson Creek; TU 75460 (1): MS, Hinds Co., Big Black River; TU 78730 (1): MS, Lincoln Co., Homochitto River; TU 84066 (1): MS, Copiah Co., Homochitto River; TU 91107 (1): MS, Hinds Co., Tallahala Creek; TU 91201 (4): MS, Copiah Co., Foster Creek; TU 124195 (1): MS, Lincoln Co., Homochitto River. Pearl River Dr.: TU 17652 (3): MS, Marion Co., Pearl River; TU 26537 (1): MS, Marion Co., Harvey Creek; TU 26601 (1): LA, St. Tammany Par., Talley's Creek; TU 28920 (1): MS, Marion Co., Trib. to Pearl River; TU 36048 (2): LA, Washington Par., Talisheek Creek; TU 50186 (1): LA, Washington Par., Pearl River; TU 53615 (1): MS, Simpson Co., Strong River; TU 54389 (2): MS, Simpson Co., Strong River; TU 55521 (2): MS, Simpson Co., Strong River; TU 56069 (4): MS, Simpson Co., Strong River; TU 56489 (1): MS, Simpson Co., Strong River; TU 56611 (2): MS, Simpson Co., Strong River; TU 57437 (1): LA, Washington Par., Pearl River; TU 58215 (3): MS, Simpson Co., Strong River; TU 59264 (2): MS, Simpson Co., Strong River; TU 62465 (1): MS, Simpson Co., Strong River; TU 64472 (1): MS, Simpson Co., Strong River; TU 170514 (1): MS, Lincoln Co., Fair River. Pascagoula River Dr.: TU 4284 (19): MS, Jasper Co., Minnows Inc. Hatchery; TU 55480 (1): MS, Covington Co., Okatoma Creek; TU 56653 (1): MS, Jones Co., Leaf River; TU 66040 (2): MS, Jones Co., Leaf River. Tombigbee River/lower Black Warrior: AUM 19506 (1): AL, Greene Co., Gainesville Lake; GSA 6607.05 (3): AL, Tuscaloosa Co., Little Tyro Creek; GSA 6619.03 (2): AL, Tuscaloosa Co., Little Tyro Creek; GSA 6848.06 (10): AL, Tuscaloosa Co., Little Tyro Creek; GSA 6855.06 (8): AL, Tuscaloosa Co., Little Tyro Creek; GSA 7000.07 (2): AL, Tuscaloosa Co., Little Tyro Creek; GSA 7204.09 (2): AL, Tuscaloosa Co., Little Tyro Creek; GSA 7249.08 (3): AL, Tuscaloosa Co., Kepple Creek; GSA 7384.11 (7): AL, Tuscaloosa Co., Kepple Creek; GSA 7393.11 (7): AL, Tuscaloosa Co., Kepple Creek; GSA 7496.14 (2): AL, Hale Co., German Creek; GSA 7560.11 (2): AL, Greene Co.,

Minter Creek; TU 76977 (36): AL, Greene Co., Needham Creek; UAIC 1541.01 (7): AL, Tuscaloosa Co., seepage pool. Alabama River: AUM 6791 (5): AL, Lee Co., Trib. to Choctafaula Creek; AUM 10885 (8): AL, Macon Co., Sandy Creek; AUM 19968 (1): AL, Macon Co., Opintloco Creek; AUM 23151 (1): AL, Lowndes Co., temporary pond; AUM 27682 (1): AL, Lowndes Co., Dry Cedar Creek; TU 35057 (11): AL, Dallas Co., Oakmulgee Creek; TU 35142 (1): AL, Dallas Co., Pine Flat Creek; TU 70675 (1): AL, Wilcox Co., Alabama River; TU 163142 (1): AL, Wilcox Co., Alabama River. Perdido River Dr.: TU 23980 (1): AL, Escambia Co., Brushy Creek. Escambia River Dr.: AUM 20999 (4): AL, Covington Co., Blue Spring. Choctawhatchee River Dr.: AUM 4693 (30): AL, Barbour Co., Easterling Fish Hatchery. Apalachicola River Dr.: AUM 1285 (1): AL, Russell Co., Snake Creek; AUM 2850 (19): AL, Lee Co., Trib. to Flake Creek; AUM 9266 (1): AL, Lee Co., Flake Creek; AUM 10749 (3): AL, Lee Co., Trib. to Little Uchee Creek; AUM 10815 (3): AL, Lee Co., White's Creek; AUM 13373 (1): AL, Russell Co., Padgett Branch; AUM 15153 (1): AL, Lee Co., Trib. to Little Uchee Creek; AUM 24067 (1): AL, Lee Co., Trib. to Uchee Creek. Altamaha River Dr.: Uncataloged (1): GA, Butts Co., Plymale Creek; AUM 10370 (5): GA, Ben Hill Co., Merritts Pond; AUM 14212 (1): GA, Dekalb Co., Swift Creek.

DIAGNOSIS: A species of subgenus *Fuscatelum*, as diagnosed herein and by Page (1981), differing from the only other recognized species in the subgenus, *E. phytophilum*, in usually having 48 or more lateral line scales (lateral line scales usually 47 or lower in *E. phytophilum*), 14 or more transverse scales (tranverse scales usually 13 or lower in *E. phytophilum*), and 23 or more caudal peduncle circumferential scales (caudal penduncle scales usually 22 or lower in *E. phytophilum*). The lateral line in females and non-breeding males is distinctly depigmented, especially anteriorly (not distinctly depigmented in *E. phytophilum*.).

DESCRIPTION: *E. parvipinne* is a moderate-sized species of genus *Etheostoma*, similar in size to *E. phytophilum*: the average size of 376 specimens examined in this study (none less than 30 mm SL) is 38.78 mm SL; maximum size, 55 mm SL. Lateral line scales 42–66 (usually 48 or more, Table 1), of which 33 to 61 are pored (Table 2); transverse scale rows 11 to 18 (usually 14 or more, Table 3); caudal peduncle circumferential scales 20–30 (usually 23 or more, Table 4). The combination of 48 or more lateral line scales, 14 or more transverse scales, and 23 or more caudal peduncle scales characterizes 93% of the specimens of *E. parvipinne* examined. Nape, cheeks, opercle, prepectoral area, breast and anterior belly fully scaled (scales sometimes partly embedded). First dorsal fin with 7 to 14 (usually 9 or 10) spines (Table 5); second dorsal fin with 9 to 13 (usually 10 or 11) soft rays (Table 6); right pectoral rays 13 to 17, (usually 15 or 16, Table 7); pelvic fin invariant with one spine and 5 soft rays; anal fin with two spines (one sometimes reduced) and 7 to 10 (usually 8 or 9) soft rays (Table 8); caudal fin with 10–16 branched rays (12–16 principal rays, Table 9). Vertebrae 34–38.

Etheostoma parvipinne is nearly identical to *E. phytophilum* in characters of the lateral canal (complete with 5 pores), supratemporal canal (incomplete with two pores); supraorbital canal (complete with four pores); coronal pore (present); infraorbital canal (complete with 3–10 pores, Table 10); and preoperculomandibular canal (complete with 6–12 pores, Table 11).

Color in life taupe (brownish gray), with darker brown pigment forming a distinctive pattern over a lighter yellow to whitish body color. Dark brown pigment

also covers most of upper sides of the head and body. A somewhat darker brown stripe runs from top of opercle, through eye, along snout and onto upper jaw. A thick, brown bar runs vertically from eye to underside of the head. Side of head below the lateral eye stripe light yellow to white, although the entire area may be flecked with melanophores in densely pigmented specimens. Lower jaw and chin also light with brown flecking. Brown pigment on body either diffuse or producing a dense brown mottling that dissipates ventrally. Brown pigment forms a series of 8–10 irregular dashes along the mid sides, which may be drawn into vertical bars in breeding males. The bars are sometimes confluent, forming a brown mid-lateral stripe. The lateral line is distinctly depigmented along most of its length just above the mid-lateral dashes, producing the "gold stripe" typical of the species. The stripe is sometimes obliterated by brown pigment on the sides of the body. As many as 10 narrow saddles may cross the top of the back generally in line with the vertical bars.

Medial fins have a varying number of wavy bands of brown pigment. The bands are most numerous on the caudal fin and least developed on the anal fin. Most of the pigment forming the bands is along the edges of individual fin rays; fin membranes adjacent to the bands have only a scattering of melanophores, making the bands appear interrupted. Two to as many as four dark brown spots may be seen at the base of the caudal fin. Paired fins without pigment, except in breeding males.

As described for the rush darter and subgenus *Fuscatelum*, the body and fins of breeding male goldstripe darters become dusky during the breeding season. A concentrated spot of black pigment forms in the anterior portion of the spinous dorsal fin. The rest of the fin is dusky except for a pigmentless strip along the distal margin. Breeding males of *E. parvipinne* differ from *E. phytophilum* in sometimes having the midlateral dashes extended into a series of dark vertical bars that are generally in line with the saddles crossing the back. This pigmentation pattern has been associated with aggressive encounters (Johnston 1994). When present, the bars obliterate the gold stripe running along the side. Male breeding tubercles, and male and female genital papillae are as described for *E. phytophilum*. No tubercular ridges were observed on the pelvic fin as noted by Richards (1963).

VARIATION: Scale counts exhibit the greatest variability east to west across the range of *E. parvipinne*. Populations from the Colorado River system in Texas, eastward to the Alabama River, AL vary more or less as a group, and tend to have higher means for all scale counts. Counts tend to be slightly lower for populations in upper portions of the Mississippi River Valley (Obion and Tennessee river systems), and highly variable for populations in the Tombigbee and lower Black Warrior river systems. A more pronounced shift toward lower scale counts occurs east of Mobile Bay, especially Choctawhatchee River to Altamaha River. The counts approach the condition seen in *E. phytophilum*. Sample sizes are too small to judge how well the Perdido and Escambia river populations fit this pattern. A pattern of vicariance involving divergence of populations east of Mobile Bay from a more widespread, western group of populations extending to or including the Mississippi River, has been observed for a number of other groups of fishes (Wiley and Mayden, 1985).

DISTRIBUTION: *Etheostoma parvipinne* is primarily restricted to lowland streams on

the Coastal Plain, below the Fall Line. The species occurs from the Colorado River drainage in Texas, east to the Altamaha River drainage in Georgia (the only Atlantic Slope population), and in lowland tributaries of the Mississippi River northward as far as extreme southern Missouri and Kentucky (northern extent of the Mississippi Embayment, Figure 1). *E. parvipinne* occurs above the Fall Line only in the Ocmulgee River system (Altamaha River drainage) the easternmost extent of the distribution. The Brazos River was believed to be the westernmost limit of the distribution (Rohde, 1980). However, Doyle T. Mosier recently discovered a population in Alum Creek in the Colorado River drainage. Counts from these specimens are included in comparisons.

HABITAT AND BIOLOGY: The goldstripe darter generally inhabits very small streams, spring runs, and seeps, where the water is clear, current is slow to moderate, and the substrate is silt, sand or clay. It is usually associated with aquatic vegetation. The goldstripe darter frequently colonizes small ponds, apparently entering these water bodies from small, vegetated tail waters.

The peak breeding season of the goldstripe darter is March and April but may extend into May. Johnston (1994) reported on the breeding behavior of specimens of *E. parvipinne* captured in April, amid *Vallisneria* sp. along the margin of a spring in the Tallahatchie River system. The specimens were transferred to aquaria where they spawned a short time later. The following account on spawning and early life history is summarized from Johnston (1994).

Males are nonterritorial but aggressive. During spawning and aggressive interactions with other males, body coloration changes from olive brown (sometimes with dark blotches) to brown with a series of black vertical bars. The suborbital bar darkens, the eyes become intensely red, the pelvic and anal fins change from dusky to black, and the dorsal fin become intensely black.

During aggressive encounters, males perform stationary, lateral displays with erect dorsal fins. Males chase females, mounting them with the caudal peduncle along the females' side when the female moves onto a spawning surface. The pair vibrates as eggs are released. Spawning is promiscuous, with both males and females spawning with more than one partner. The eggs are strongly adhesive and stick to a variety of spawning substrates in the aquarium, including plant stems, leaves, roots, rock and the sides of the aquarium. The species has the spawning attributes of an egg-attacher; that is, its eggs are relatively small and adhesive, and the genital papillae of females are long and [apically] tubular.

Fertilized, water-hardened eggs ranged from 0.85 to 1.10 mm in diameter and hatched in 8 days when incubated at 20°C. Multiple stages of egg development were observed in the ovary, indicating that more than one clutch of eggs is spawned during the course of the spawning season. The average number of ripening ova per ovary was 33. Young-of-the-year specimens (≈20 mm TL) were collected in May with two different size groups of adults (45 to 50 and 55 to 65 mm SL), suggesting the presence of three year classes.

ETYMOLOGY: *parvipinne* is derived from the Latin words parvus, meaning "small"

and pinna meaning "fin", and apparently is in allusion to the very short pectoral and pelvic fins (Gilbert 1887).

Morphometrics

Univariate comparisons.—Table 12 lists means for 14 body proportions, expressed as hundredths of standard length, for males and females of *E. phytophilum*, and topotypical *E. parvipinne* from streams tributary the Black Warrior River system in the vicinity of Tuscaloosa, AL. All of the differences mentioned below are significant at or below the 0.10 level.

Sexual dimorphism was evident in a number of body proportions, but expression differed between species. Males of *E. phytophilum* have higher means for caudal peduncle length, longest dorsal spine (height of the spinous dorsal fin), and caudal fin length than females. Males of *E. parvipinne* have higher means for snout length, longest dorsal spine and ray length, and pelvic fin length than females. The sexual dimorphism in body depth noted for *E. parvipinne* (females deeper bodied than males) is undoubtedly related to the peak breeding condition of the specimens; i.e., the abdomens of females were distended with eggs. Most of the specimens of *E. phytophilum* used in this comparison were not in peak spawning condition.

The head in *E. phytophilum* tends to be proportionately longer and deeper than that in typical *E. parvipinne* (males and females). *E. phytophilum* also has a shorter caudal peduncle, and longer caudal and pectoral fins than *E. parvipinne*. Other differences are sex specific. Male *E. phytophilum* have larger orbits that male *E. parvipinne*; however, orbit size does not differ between species in females. Similarly, females of *E. phytophilum* have shorter spinous dorsal fins and longer pelvic fins than female *E. parvipinne*, but these characters do not differ between males of the two species.

Principal Components Analysis.—Clusters representing *E. phytophilum* and *E. parvipinne* from the lower Black Warrior showed nearly complete separation in the space define by the first two components derived in the Principal Components Analysis (PCA) of body proportion data (Figure 5). Characters loading heavily on PC 1 included head length, and length of the pectoral, pelvic and caudal fins, all of which tended to be longer in *E. phytophilum* than in *E. parvipinne*. Characters loading heavily on PC 2 included caudal peduncle length, and first and second dorsal fin height, which tended to be longer and higher in *E. parvipinne* than in *E. phytophilum*.

Ackowledgments

For assistance in the field, we thank Royal Suttkus, Joseph Buckley, Clark Gradney, and Mark Bailey. We thank the following individuals for loans of specimens under their care: Rick Mayden and Bernie Kuhajda, University of Alabama Ichthyological Collection; Brooks Burr, Southern Illinois University; Maurice F. Mettee Jr.,

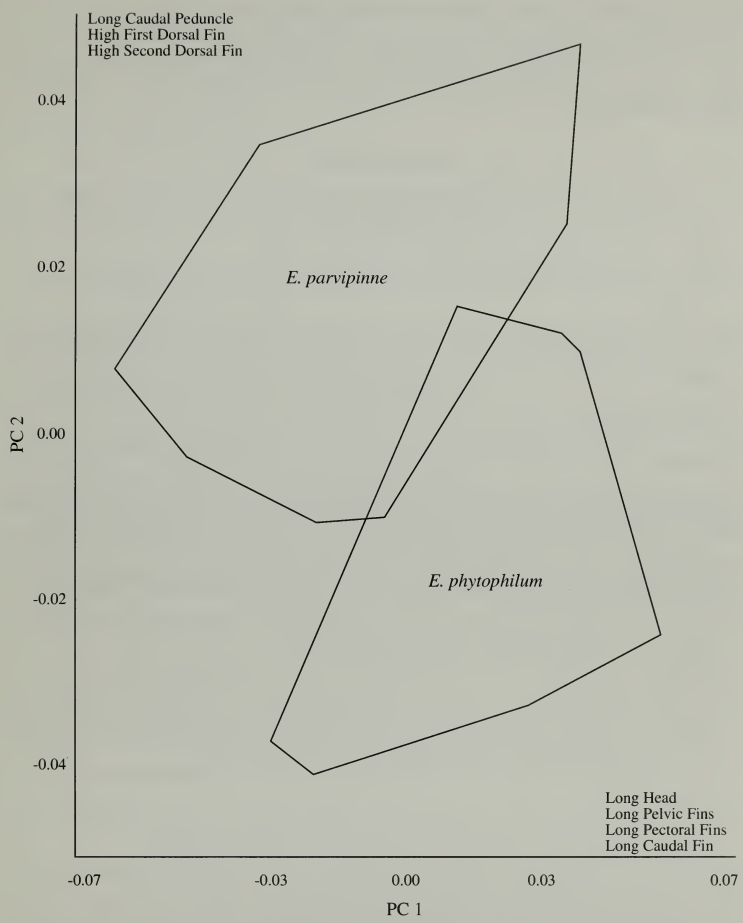

Figure 5. PCA Polygons representing projections of morphometric data for *E. parvipinne* and *E. phytophilum* on the first two principal components. Body proportions loading heavily on these components and the direction of variation are shown along the axes.

Geological Survey of Alabama; and Dean Hendrickson and Allison Anderson Texas Memorial Natural History Museum. We also thank Jon Armbruster for allowing us to distribute specimens from a type lot cataloged in the Auburn University Museum Fish Collection, and Stuart Poss for use of radiographic equipment at Gulf Coast Research Laboratory. Lastly, we thank Bob Cashner for serving as referee on reviews, and two anonymous reviewers for editorial suggestions that improved the quality of the paper.

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Table 1. Frequency distribution of lateral-line scale counts in *Etheostoma phytophilum* and across the range of E. *parvipinne*.

	38–39	40–41	42–43	44–45	46–47	48–49	50–51	52–53	54–55	56–57	58–59	60–61	62–63	66–67	N	$\bar{x}$	SD
E. parvipinne																	
Colorado River						6	3	4	1						14	49.71	2.05
Brazos River									1						1	54.00	
San Jacinto River				1	1	3	13	6	4	2					30	50.43	2.56
Sabine River						1	6	4	1	1					13	50.77	2.13
Red River					1	4	3	5	3	4	2	1			23	52.09	3.86
Obion River			1	8	10	8	3								30	45.80	2.11
Tennessee River				7	2	2	3	5		2	1				22	48.45	4.39
Lower Mississippi R.						2	7	5	9	3	4		1		32	52.59	3.40
Pearl River						1	3	10	6	9				1	30	53.13	3.42
Pascagoula River							4	8	7	3					23	52.52	2.23
Tombigbee/Warrior			1	1	1	10	6	12	10	8	1	2	2		56	52.07	4.19
Alabama River				4	5	8	6	4	2		1				30	48.47	3.52
Perdido River						1									1	47.00	
Escambia River							1	2	1						4	51.75	1.71
Choctawhatchee R.				2	1	11	10	4	2						30	48.73	2.29
Apalachicola River			1	7	11	5	4	2							30	46.23	2.60
Altamaha River	1			1		1	2		1						6	46.57	4.86
E. phytophilum																	
Clear Creek		1	6	10	15	5	5								42	46.07	2.34
Turkey Creek	1	2	8	10	4										25	43.68	2.79
Little Cove Creek		1													1	40.00	

Table 2. Frequency distribution of pored lateral line scale counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	32–33	34–35	36–37	38–39	40–41	42–43	44–45	46–47	48–49	50–51	52–53	54–55	56–57	59–60	62–63	N	$\bar{x}$	SD
E. parvipinne																		
Colorado River							2	5	2	4		1				14	47.29	2.70
Brazos River												1				1	53.00	
San Jacinto River					4	1	7	5	6	3	2	2				30	45.90	3.88
Sabine River						1	1	3	4	3	1					13	47.23	2.59
Red River						2	3	2	3	5	2	4	2			23	48.78	4.36
Obion River		1	2	1	7	7	5	6		1						30	41.63	3.44
Tennessee River		1			3	6	2	2	4	3		1				22	44.09	4.47
Lower Mississippi R.					1		2	4	8	6	7	3	1			32	48.88	3.30
Pearl River				1		1	1	3	3	8	8	4			1	30	49.63	4.28
Pascagoula River				1			1	2	7	6	3	2	1			23	48.70	3.61
Tombigbee/Warrior				1	1	3	3	6	6	13	12	4	4	2	1	56	49.34	4.59
Alabama River						1	8	3	9	2	5	2				30	47.07	3.25
Perdido River								1								1	45.00	
Escambia River									1	2	1		1			4	49.50	1.29
Choctawhatchee R.				1	3	7	1	9	5	4	1					30	44.67	3.47
Apalachicola River				1	3	6	5	11	2	1						30	43.87	3.07
Altamaha River			1			1	1		2	2						7	45.00	5.03
E. phytophilum																		
Clear Creek	1			4	6	7	13	6	4	1						42	43.57	3.20
Turkey Creek	1	2	7	8	6	1			2	2						25	37.92	4.23
Little Cove Creek				1												1	37.00	

Table 3. Frequency distribution of transverse scale counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	10	11	12	13	14	15	16	17	18	N	$\bar{x}$	SD
E. parvipinne												
Colorado River			2	5	3	3	1			14	13.71	1.20
Brazos River							1			1	16.00	
San Jacinto River				3	7	12	7	1		30	14.87	1.01
Sabine River					4	4	4	1		13	15.15	0.99
Red River					1	2	14	5	1	23	16.13	0.81
Obion River			5	15	6	4				30	13.30	0.92
Tennessee River				13	6	3				22	13.55	0.74
Lower Mississippi R.				6	10	14	2			32	14.38	0.87
Pearl River				2	2	20	6			30	15.00	0.74
Pascagoula River				3	9	9	2			23	14.43	0.84
Tombigbee/Warrior			1	7	23	21	4			56	14.36	0.86
Alabama River			1	10	14	5				30	13.77	0.77
Perdido River					1					1	14.00	
Escambia River			2	1	1					4	12.75	0.96
Choctawhatchee R.			6	12	9	2				30	13.24	0.87
Apalachicola River		4	4	21	1					30	12.63	0.76
Altamaha River			1	5	1					7	13.00	0.58
E. phytophilum												
Clear Creek		1	24	15	2					42	12.43	0.69
Turkey Creek	1		9	15						25	12.52	0.74
Little Cove Creek				1						1	13.00	

Table 4. Frequency distribution of caudal peduncle circumferential scale counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	18	19	20	21	22	23	24	25	26	27	28	29	30	N	$\bar{x}$	SD
E. parvipinne																
Colorado River						2	4	4	2	2				14	24.86	1.29
Brazos River									1					1	26.00	
San Jacinto River						1	7	11	5	5	1			30	25.30	1.21
Sabine River							1	4	4	3		1		13	26.00	1.29
Red River							3	2	3	6	6	1	2	23	26.91	1.73
Obion River				3	7	9	4	6	1					30	23.20	1.37
Tennessee River				2	4	11	2	1	2					22	23.09	1.31
Lower Mississippi R.					2	6	6	12	4	1		1		32	24.56	1.46
Pearl River					1	3	5	1	7	7	5			30	25.76	1.79
Pascagoula River					1	4	8	6	1	3				23	24.48	1.34
Tombigbee/Warrior			1	3	5	5	12	9	15	2	3	1		56	24.61	1.94
Alabama River						2	6	9	5	7		1		30	25.43	1.41
Perdido River							1							1	24.00	
Escambia River				1	1		2							4	22.75	1.50
Choctawhatchee R.						5	6	8	7	1	2			30	24.97	1.40
Apalachicola River			1	5	8	9	5	1	1					30	22.63	1.33
Altamaha River			1			1	3	1		1				7	23.86	2.12
E. phytophilum																
Clear Creek	2	2	12	17	9									42	20.69	1.27
Turkey Creek		2	4	12	7									25	20.96	1.05
Little Cove Creek			1											1	20.00	

Table 5. Frequency distribution of dorsal spine counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	7	8	9	10	11	12	13	14	N	$\bar{x}$	SD
E. parvipinne											
Colorado River			7	7					14	9.50	0.52
Brazos River			1						1	9.00	
San Jacinto River		1	16	11	2				30	9.47	0.68
Sabine River	1	4	7	1					13	8.62	0.77
Red River		5	10	7	1				23	9.17	0.83
Obion River		1	4	15	8	1		1	30	10.27	1.08
Tennessee River			5	7	8	2			22	10.32	0.95
Lower Mississippi R.		4	10	11	7				32	9.66	0.97
Pearl River		2	10	16		2			30	9.67	0.88
Pascagoula River			2	3	11	6	1		23	11.04	0.98
Tombigbee/Warrior		3	24	25	4				56	9.54	0.71
Alabama River		1	13	14	2				30	9.50	0.82
Perdido River			1						1	9.00	
Escambia River			1	2	1				4	10.00	0.82
Choctawhatchee R.		1	1	26	1				30	9.93	0.46
Apalachicola River		1	8	19	2				30	9.73	0.64
Altamaha River			2	3	1	1			7	10.14	1.07
E. phytophilum											
Clear Creek		3	16	18	5				42	9.60	0.82
Turkey Creek		3	5	17					25	9.56	0.69
Little Cove Creek				1					1	10.00	

Table 6. Frequency distribution of dorsal ray counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	9	10	11	12	13	N	$\bar{x}$	SD
E. parvipinne								
Colorado River		8	6			14	10.43	0.51
Brazos River		1				1	10.00	
San Jacinto River	1	16	13			30	10.40	0.56
Sabine River		5	7	1		13	10.70	0.63
Red River	1	11	10	1		23	10.48	0.67
Obion River		12	16	1	1	30	10.70	0.70
Tennessee River		7	11	4		22	10.86	0.71
Lower Mississippi R.	3	20	7	2		32	10.25	0.72
Pearl River	1	12	16	1		30	10.57	0.63
Pascagoula River	1	4	14	4		23	10.91	0.73
Tombigbee/Warrior	1	14	26	13	1	56	10.98	0.80
Alabama River	3	13	12	1	1	30	10.47	0.86
Perdido River		1				1	10.00	
Escambia River		3	1			4	10.25	0.50
Choctawhatchee R.	7	17	5			30	9.93	0.65
Apalachicola River	3	22	5			30	10.07	0.52
Altamaha River		4	3			7	10.43	0.53
E. phytophilum								
Clear Creek		24	16	2		42	10.48	0.65
Turkey Creed	1		10	13	1	25	11.52	0.78
Little Cove Creek			1			1	11.00	

Table 7. Frequency distribution of right pectoral ray counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	12	13	14	15	16	17	N	$\bar{x}$	SD
E. parvipinne									
Colorado River				5	9		14	15.64	0.50
Brazos River			1				1	14.00	
San Jacinto River		3	14	9	4		30	14.47	0.86
Sabine River		1	1	6	5		13	15.15	0.90
Red River			2	15	5	1	23	15.22	0.67
Obion River		1	4	16	9		30	15.10	0.76
Tennessee River				14	8		22	15.36	0.49
Lower Mississippi R.				20	10	2	32	15.44	0.62
Pearl River			1	15	14		30	15.43	0.57
Pascagoula River			3	11	9		23	15.26	0.69
Tombigbee/Warrior			12	37	6	1	56	14.93	0.63
Alabama River	1		3	13	10	3	30	15.33	1.03
Perdido River					1		1	16.00	
Escambia River			2		2		4	15.00	1.15
Choctawhatchee R.			2	17	10		30	15.28	0.59
Apalachicola River		1	2	14	13		30	15.30	0.75
Altamaha River			1	2	4		7	15.43	0.79
E. phytophilum									
Clear Creek			3	16	23		42	15.48	0.68
Turkey Creek			14	11			25	14.44	0.67
Little Cove Creek					1		1	16.00	

Table 8. Frequency distribution of anal ray counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	7	8	9	10	N	$\bar{x}$	SD
E. parvipinne							
Colorado River	7	7			14	7.50	0.52
Brazos River		1			1	8.00	
San Jacinto River		12	18		30	8.60	0.50
Sabine River	1	8	3	1	13	8.31	0.75
Red River	2	15	6		23	8.17	0.58
Obion River		4	22	4	30	9.00	0.53
Tennessee River		7	14	1	22	8.73	0.55
Lower Mississippi R.	3	18	11		32	8.25	0.62
Pearl River	8	18	4		30	7.87	0.63
Pascagoula River	1	8	12	2	23	8.65	0.71
Tombigbee/Warrior	3	23	26	3	56	8.53	0.69
Alabama River	5	22	3		30	7.93	0.52
Perdido River	1				1	7.00	
Escambia River		2	2		4	8.50	0.58
Choctawhatchee R.	3	24	2		30	7.97	0.42
Apalachicola River	9	20	1		30	7.73	0.52
Altamaha River		5	2		7	8.29	0.49
E. phytophilum							
Clear Creek		14	24	4	42	8.76	0.64
Turkey Creek	1	6	15	3	25	8.80	0.66
Little Cove Creek				1	1	10.00	

Table 9. Frequency distribution of branched caudal ray counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	10	11	12	13	14	15	16	N	$\bar{x}$	SD
E. parvipinne										
Colorado River				5	6	3		14	13.86	0.77
Brazos River					1			1	14.00	
San Jacinto River			3	8	10	7		28	13.75	0.97
Sabine River			1	1	9	2		13	13.92	0.76
Red River			2	8	12	1		23	13.52	0.73
Obion River		2	7	20	1			30	12.67	0.66
Tennessee River		1	2	7	7	3	1	22	13.57	1.16
Lower Miss. R.			1	8	15	6	1	31	13.93	0.85
Pearl River	2	1	2	3	14	8		30	13.67	1.40
Pascagoula River			1	7	10	5		23	13.83	0.83
Tombigbee/Warrior		1	4	27	16	7		56	13.44	0.88
Alabama River			1	6	16	7		30	13.97	0.76
Perdido River						1		1	15.00	
Escambia River				2	2			4	13.50	0.58
Choctawhatchee R.				15	7	7		30	13.72	0.84
Apalachicola River	1	1	3	3	14	8		30	13.73	1.26
Altamaha River			1	5	1			7	13.00	0.58
E. phytophilum										
Clear Creek			3	12	16	11		42	13.83	0.95
Turkey Creek		1	5	17	2			25	12.80	0.84
Little Cove Creek			1					1	12.00	

Table 10. Frequency distribution of infraorbital pore counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	3	5	6	7	8	9	10	N	$\bar{x}$	SD
E. parvipinne										
Colorado River				4	9	1		14	7.79	0.58
Brazos River					1			1	8.00	
San Jacinto River				2	24	4		30	8.07	0.45
Sabine River				3	8	2		13	7.92	0.64
Red River		1		3	19			23	7.74	0.69
Obion River			1	4	23	2		30	7.87	0.57
Tennessee River				2	19	1		22	7.95	0.38
Lower Miss. R.			1		25	5	1	32	8.16	0.63
Pearl River	1			3	23	3		30	7.83	1.02
Pascagoula River				2	18	3		23	8.04	0.47
Tombigbee/Warrior				9	43	4		56	7.91	0.48
Alabama River				5	23	2		30	7.90	0.48
Perdido River				1				1	7.00	
Escambia River					4			4	8.00	
Choctawhatchee R.				1	22	6		30	8.17	0.47
Apalachicola River				1	27	2		30	8.03	0.32
Altamaha River				1	4	2		7	8.14	0.69
E. phytophilum										
Clear Creek		1	1	8	29	3		42	7.76	0.58
Turkey Creek				13	8	3	1	25	7.68	0.97
Little Cove Creek					1			1	8.00	

Table 11. Frequency distribution of preoperculomandibular pore counts in *Etheostoma phytophilum* and across the range of *E. parvipinne*.

	6	7	8	9	10	11	12	N	$\bar{x}$	SD
E. parvipinne										
Colorado River		1		1	9	3		14	9.93	1.00
Brazos River					1			1	10.00	
San Jacinto River				1	26	3		30	10.07	0.37
Sabine River				1	11	1		13	10.00	0.41
Red River				3	20			23	9.87	0.34
Obion River				2	27	1		30	9.97	0.92
Tennessee River			1	1	17	2	1	22	10.05	0.72
Lower Miss. R.				2	28	2		32	10.00	0.36
Pearl River	1		1	3	21	4		30	9.83	0.95
Pascagoula River				3	18	2		23	9.96	0.47
Tombigbee/Warrior		1		8	38	7	2	56	10.00	0.76
Alabama River		1	1	6	22			30	9.63	0.72
Perdido River			1					1	8.00	
Escambia River					3	1		4	10.25	0.50
Choctawhatchee R.				4	16	5	4	30	10.31	0.89
Apalachicola River				6	24			30	9.80	0.41
Altamaha River				3	4			7	9.57	0.53
E. phytophilum										
Clear Creek				9	27	5	1	42	9.95	0.70
Turkey Creek				1	24			25	9.96	0.19
Little Cove Creek					1			1	10.00	

Table 12. Means of 14 body measurements, expressed as a proportion of standard length, and ANOVA results for populations of *Etheostoma parvipinne* and *E. phytophilum*. Bold type denotes significant ($P<0.10$) sexual dimorphism for the proportion in favor of the denoted sex in within species comparisons.

	E. parvipinne		*E. phytophilum*		ANOVA Statistics			
	Lower Black Warrior River		Upper Black Warrior River		Males		Females	
Body proportion	Males (17)	Females (13)	Males (15)	Females (15)	*F*	*P*	*F*	*P*
Head length	0.270	0.265	0.277	0.273	3.33	0.078	3.25	0.083
Head Depth	0.163	0.162	0.171	0.172	9.10	0.005	4.33	0.048
Body depth	0.187	**0.196**	0.198	0.195	7.08	0.012	0.08	0.778
Body width	0.124	0.126	0.126	0.128	0.24	0.627	0.36	0.555
Caudal peduncle length	0.247	0.248	**0.229**	0.216	11.14	0.002	46.71	0.0001
Caudal peduncle depth	0.118	0.118	0.122	0.121	1.81	0.189	1.13	0.297
Snout length	**0.058**	0.054	0.057	0.054	0.24	0.627	0.15	0.703
Orbit length	0.065	0.066	0.070	0.068	7.55	0.010	2.21	0.150
Longest dorsal spine	**0.108**	0.100	**0.105**	0.089	0.69	0.413	11.45	0.002
Longest dorsal ray	**0.152**	0.145	0.150	0.145	0.22	0.643	0.00	0.980
Longest anal ray	0.140	0.140	0.139	0.136	0.03	0.858	0.97	0.333
Caudal fin length	0.213	0.212	**0.229**	0.219	9.30	0.005	2.93	0.099
Pectoral fin length	0.205	0.205	0.224	0.220	19.20	0.0001	7.22	0.012
Pelvic fin length	**0.188**	0.178	0.194	0.189	2.25	0.144	5.57	0.026

FUSCONAIA APALACHICOLA, A NEW SPECIES OF FRESHWATER MUSSEL (BIVALVIA: UNIONIDAE) FROM PRECOLUMBIAN ARCHAEOLOGICAL SITES IN THE APALACHICOLA BASIN OF ALABAMA, FLORIDA, AND GEORGIA

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Abstract

Fusconaia apalachicola, a new unionid mussel, is described from four precolumbian archaeological sites in the Apalachicola Basin. The sites range in age from A.D. 500 to 1350. *Fusconaia apalachicola* is absent from recent collections but was likely extant when Europeans arrived in North America. Its extinction was likely due to pollution and habitat destabilization resulting from agriculture and development in the Apalachicola Basin beginning in the early 1800s. This species is known only from this basin and only from archaeological contexts. It is the first species of the genus *Fusconaia* known to occur within the Apalachicola Basin. Based on conchological characters it appears to be most closely related to *F. rotulata* which is endemic to the Escambia River drainage in south Alabama and west Florida.

Introduction

Within the southeastern United States, the eastern drainages of the Gulf of Mexico harbor a diverse unionid mollusk fauna. This fauna consists of widespread taxa that occur from the Mississippi Basin eastward and south Atlantic drainages westward into the eastern Gulf (Burch, 1975). This region is also inhabited by a relatively large number of endemic mussel taxa. The endemic mussel fauna in the eastern Gulf drainages, Escambia River east to Suwannee River, consists of 26 species and one genus, *Elliptoideus* Frierson, 1927 (Butler, 1989; Williams and Butler, 1994).

Much of the eastern Gulf region endemism is centered in the Apalachicola Basin, which is drained by the Apalachicola, Chattahoochee, and Flint rivers. The Apalachicola Basin is the largest drainage east of the Mobile Basin and drains portions of eastern Alabama, western Georgia, and northwestern Florida. Within the region, the Apalachicola Basin supports the greatest number of freshwater mollusk species as well as endemics (Butler, 1989; Clench and Turner, 1956). The mussel fauna of the Basin consists of 33 species, of which 10 are endemic (Brim Box and Williams, in press).

The genus *Fusconaia* is widespread in the Mississippi Basin and Gulf of Mexico drainages where it is represented by 13 species. In the Atlantic Coast drainages,

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however, the genus *Fusconaia* is represented by a single species, *F. masoni* (Conrad, 1834) (Potomac River drainage south to the Savannah River drainage). In the eastern Gulf drainages from the Mobile Basin eastward, the genus *Fusconaia* is represented by *F. cerina* (Conrad, 1838) and *F. ebena* (Lea, 1831) (Mobile Basin and westward), *F. escambia* Clench & Turner, 1956 (Escambia and Yellow river drainages), *F. rotulata* (Wright, 1899) (Escambia River drainage), and *F. succissa* (Lea, 1852) (Escambia River drainage east to Choctawhatchee River). *Fusconaia apalachicola* n. sp. was endemic to the Apalachicola Basin, the only species of *Fusconaia* known from this basin, and was the easternmost representative of the genus on the Gulf Coast.

Fusconaia apalachicola was discovered in the process of identifying mollusks in a faunal sample from a precolumbian archaeological site located along the main channel of the upper Apalachicola River, Liberty County, northwest Florida. An additional 13 species of unionid mussels were found in archaeological samples in the Apalachicola Basin. While all 13 species are well represented in museum collections of recent mollusks, it appears that *F. apalachicola* disappeared before modern malacologists or shell collectors could collect live or fresh shells.

Materials and Methods

Comparative archaeological material of *Fusconaia apalachicola* was obtained from three museum research collections. We examined faunal collections housed in the Florida Museum of Natural History, Gainesville, Florida (FLMNH), the Bureau of Archaeological Research, Division of Historic Resources, Department of State, Tallahassee, Florida (FLBAR), and the Columbus Museum, Columbus, Georgia (uncataloged). Material of other species of *Fusconaia* was obtained from the FLMNH, the Alabama Malacological Research Center, Mobile, Alabama (AMRC), the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and U.S. Geological Survey, Gainesville, Florida collections.

Type material was designated for specimens in the collection of the FLMNH. Additional specimens from the FLBAR collections were designated as type material and deposited at the North Carolina State Museum of Natural Sciences, Raleigh, North Carolina (NCSM), the University of Tennessee McClung Museum, Knoxville, Tennessee (UTMM), and the USNM.

A total of 56 specimens of *Fusconaia apalachicola* was identified in the FLMNH precolumbian archaeological sample from Site 8LI76, Liberty County, Florida. We also identified specimens of *F. apalachicola* in the FLBAR collections from the Sycamore Site 8GD13, Gadsden County, Florida, and from the Scholz Steam Plant Site 8JA104, Jackson County, Florida. Of the specimens examined, we borrowed 24 of the most complete valves for comparative study, 14 from the Sycamore Site and 10 from the Scholz Steam Plant Site. These three sites were located along the main channel in the upper reach of the Apalachicola River (Figure 1).

We also examined material from the Chattahoochee and Flint rivers housed in the Columbus Museum, Georgia. One additional specimen of *Fusconaia apalachicola* was found in a faunal sample from the Omussee Creek Site 1HO26, Houston County, southeast Alabama (Figure 1). This specimen is the only record from the Chattahoochee River and the only occurrence of the species outside the state of Florida.

Figure 1. Distribution of *Fusconaia apalachicola* (stars) in the Chattahoochee River system, Alabama and Georgia, and in the Apalachicola River system, Florida, and *Fusconaia rotulata* (triangles) in the Escambia River drainage, Alabama and Florida.

None of the valves of *Fusconaia apalachicola* were complete, although many were missing only a small portion of the posterior end of the shell. Also, there was only a trace of periostracum on a few of the archaeological specimens. The lack of complete valves prevented us from taking total length measurements for comparative purposes. Instead of using total length of the shell, we utilized a measurement of the inter-adductor muscle scar distance taken from the anterior margin of the anterior adductor mussel scar to the anterior margin of the posterior mussel scar. These landmarks were chosen because they were moderately distinct and represented the only measurement of length that could be taken with any degree of accuracy. The width of the shell was taken by measuring the maximum extent of inflation in one valve. The interdentum was used as a base for this measurement as it provided a relatively flat platform to rest one arm of the calipers. This measurement was difficult to obtain on the archaeological material since a portion of the posterior and/or

ventral margin was usually missing. Measurements were taken on both left and right valves. Dial calipers were used to take all measurements which were rounded off to the nearest tenth of a millimeter.

Fusconaia apalachicola, new species
Apalachicola ebonyshell
Figures 2a and 2b

Fusconaia sp. or *Fusconaia* cf. *rotulata*, Fradkin (1995a).
Quincuncina infucata (in part) Percy (1976).
Fusconaia succissa, *Quincuncina burkei*, and *Q. infucata* (in part) Milanich (1974).

HOLOTYPE: FLMNH 05260690.1 (left valve). Florida, Liberty County, Site 8LI76, located 500 m east of the Apalachicola River (T1N; R8W; SE 1/4 Sec. 1) near river mile 88 (U.S. Army Corps of Engineers), about 5 miles N of Bristol (Figure 2a).

PARATYPES: *Malacological Collections*.—Florida, Gadsden County, Sycamore Site 8GD13, located near the east bank of the Apalachicola River, at N 30°37'39" latitude and W 84°53'46" longitude: FLMNH 271727 (formerly cataloged as FLBAR 74.68.53.1 [right valve]); NCSM 4694 (formerly cataloged as FLBAR 74.68.156.3 [right valve]; FLBAR 74.68.156.4 [left valve]); NCSM 4695 (formerly cataloged as FLBAR 74.68.168.1 [left valve]; FLBAR 74.68.168.2 [left valve]; FLBAR 74.68.168.3 [left valve]); USNM 880618 (formerly cataloged as FLBAR 74.68.150.1 [right valve]; FLBAR 74.68.150.2 [right valve]); USNM 880617 (formerly cataloged as FLBAR 74.68.157.1 [left valve]); UTMM 3410 (formerly cataloged as FLBAR 74.68.157.2 [right valve]; FLBAR 74.68.158.1 [right valve]; FLBAR 74.68.158.2 [left valve]; FLBAR 74.68.158.3 [left valve]).

Florida, Jackson County, Scholz Steam Plant Site 8JA104, located near the west bank of the Apalachicola River, 3.25 miles southeast of Sneads (T3N; R7W; SW 1/4 Sec. 12): FLMNH 271728 (formerly cataloged as FLBAR 75.138.01.1 [left valve]).

Archaeological Collections.—Florida, Liberty County, Site 8LI76, located 500 m east of the Apalachicola River (T1N; R8W; SE 1/4 Sec. 1) at river mile 88 (U.S. Army Corps of Engineers), about 5 miles N of Bristol: FLMNH 05260528.1 (right valve); FLMNH 05260528.2 (right valve); FLMNH 05260528.3 (left valve); FLMNH 05260528.4 (right valve); FLMNH 05260528.5 (left valve); FLMNH 05260528.6 (left valve); FLMNH 05260528.7 (left valve); FLMNH 05260528.8 (right valve); FLMNH 05260528.9 (right valve); FLMNH 05260528.10 (right valve); FLMNH 05260528.11 (right valve); FLMNH 05260560.1 (left valve); FLMNH 05260560.2 (right valve); FLMNH 05260560.3 (right valve); FLMNH 05260560.4 (right valve); FLMNH 05260560.5 (left valve); FLMNH 05260560.6 (right valve); FLMNH 05260690.2 (right valve); FLMNH 05260690.3 (right valve).

Florida, Jackson County, Scholz Steam Plant Site 8JA104, located near the west bank of the Apalachicola River, 3.25 miles southeast of Sneads (T3N; R7W; SW 1/4 Sec. 12): FLBAR 75.138.01.2 (right valve); FLBAR 75.138.01.3 (right valve); FLBAR 75.138.01.4 (left valve); FLBAR 75.138.01.5 (left valve); FLBAR 75.138.01.6 (left valve); FLBAR 75.138.01.7 (right valve); FLBAR 75.138.01.8 (right valve).

Figure 2. A) *Fusconaia apalachicola*. Holotype, FLMNH 05260690.1 (right valve). Florida, Liberty County, Site 8LI76, located 500 m east of the Apalachicola River (T1N; R8W; SE ¼ Sec. 1) near river mile 88, about 5 miles N of Bristol, Florida. B) *Fusconaia apalachicola*. Paratype, FLMNH 05260528.9 (right valve). Florida, Liberty County, Site 8LI76, located 500 m east of the Apalachicola River (T1N; R8W; SE ¼ Sec. 1) near river mile 88, about 5 miles N of Bristol, Florida. Photo © by Richard Bryant.

Other material examined but not designated as types: Alabama, Houston County, Omussee Creek Site 1HO26, located at the mouth of Omussee Creek (Area I NW slope) where it joins the Chattahoochee River, at Columbia, Alabama: uncataloged, Columbus Museum, Georgia (left valve). Florida, Liberty County, Site 8LI76, located 500 m east of the Apalachicola River (T1N; R8W; SE ¼ Sec. 1) at river mile 88 (U.S. Army Corps of Engineers), about 5 miles N of Bristol: FLMNH 05260585.1 (right valve); FLMNH 05260585.2 (left valve); FLMNH 05260585.3 (left valve); FLMNH 05260603.1 (right valve); FLMNH 05260603.2 (left valve); FLMNH 05260603.3 (left valve); FLMNH 05260603.4 (right valve); FLMNH 05260603.5 (left valve); FLMNH 05260603.6 (left valve); FLMNH 05260603.7 (left valve); FLMNH 05260603.8 (left valve); FLMNH 05260603.9 (left valve); FLMNH 05260603.10 (left valve); FLMNH 05260631.1 (right valve); FLMNH 05260631.2 (right valve); FLMNH 05260631.3 (left valve); FLMNH 05260647.1 (left valve); FLMNH 05260647.2 (right valve); FLMNH 05260647.3 (right valve); FLMNH 05260647.4 (right valve); FLMNH 05260647.5 (left valve); FLMNH 05260660.1 (right valve); FLMNH 05260702.1 (left valve); FLMNH 05260718.1 (right valve); FLMNH 05260718.2 (left valve); FLMNH 05260724.1 (right valve); FLMNH 05260724.2 (left valve). Florida, Jackson County, Scholz Steam Plant Site 8JA104, located near the west bank of the Apalachicola River, 3.25 miles southeast of Sneads (T3N; R7W; SW ¼ Sec. 12): FLBAR 75.138.02.1 (left valve); FLBAR 75.138.02.2 (right valve). Florida, Gadsden County, Sycamore Site 8GD13, located near the east bank of the Apalachicola River, at North 30°37'39" latitude and West 84°53'46" longitude: FLBAR 74.68.164.1 (right valve).

Diagnosis: *Fusconaia apalachicola* can be distinguished from other species of *Fusconaia* by the following characteristics. *Fusconaia apalachicola* has a smooth shell, lacks any trace of a posterior ridge, moderately compressed, valve depth about 2.4 times into inter-adductor muscle scar distance, circular in outline, hinge plate broad and angular, and the beak cavity is deep and compressed (Figures 2a and 2b). *Fusconaia*

succissa has a poorly defined broadly rounded posterior ridge, moderately inflated, the shell is oval in outline, rounded anteriorly, broadly convex posteriorly, hinge plate broad and arcuate, and the beak cavities are moderately deep and open. *Fusconaia escambia* has a well developed posterior ridge ending in a point posteriorly, the hinge plate is broad and strongly arcuate, and the beak cavities are moderately deep and open. The posterior slope is slightly concave. *Fusconaia rotulata* is moderately inflated and has a faint posterior ridge with one or two additional ridges on the posterior slope. Outline of the shell circular to oval, typically oval, beak cavities are moderately deep and compressed, and the hinge plate is broad and angular.

Fusconaia apalachicola has been misidentified as *Quincuncina infucata*, the sculptured pigtoe, by Milanich (1974) and Percy (1976). This species has a moderately thick shell, subcircular in outline, and moderately inflated. Surface of shell varies from almost smooth to faintly sculptured with small nodules or nodulous ridges arranged in chevron-shaped pattern. Posterior slope flat to slightly concave; the posterior ridge narrowly rounded, shell tapering to a blunt point on the base line posteriorly. The beak cavities are shallow, compressed.

DESCRIPTION: *Fusconaia apalachicola* is characterized by a smooth moderately thick shell, lack of a posterior ridge, circular in outline, compressed, and with beaks (eroded in all individuals in this sample) anterior to the center of the shell. Internally the beak cavities are deep and compressed, and the interdentum is broad and smooth. There are two thick pseudocardinals in the left valve. The crest of the dorsal pseudocardinal tooth ranges from parallel to the lateral teeth to a slightly anterior-dorsal/posterior-ventral orientation. The crest of the ventral pseudocardinal tooth is tangential to or passes through the posterior margin of the anterior adductor muscle scar. There is a single pseudocardinal in the right valve. The laterals are typically straight, but may be slightly curved, two in the left valve and one in the right valve. While nacre color cannot be determined with certainty on archaeological material, there has been no indication that it was colored. The periostracum remained partially intact on two individuals and appeared to be black.

The two best characters for distinguishing *Fusconaia apalachicola* (Figure 2) from *F. rotulata* (Figure 3) are its circular outline and more compressed shell. In *F. apalachicola* the ratio of valve depth to inter-adductor muscle scar distance ranges from 2.2 to 2.7 with a mean of 2.4 (N=20). The ratio of valve depth to inter-adductor muscle scar distance in *F. rotulata* ranges from 1.9 to 2.4 with a mean of 2.1 (N=13). The relationship of shell width and length are presented in Figure 4. Use of outline and degree of compression of the shell for taxonomic purposes in unionids, however, is often viewed with skepticism as these characters can be influenced by environment. In headwater populations of some species the shell is more compressed and round in shape when compared to downstream populations (Ball, 1922; Ortmann, 1920). However, our use of these characters in distinguishing *F. rotulata* from *F. apalachicola* is appropriate as both species occur in similar environments, the main channel of the lower portions of large rivers on the lower Coastal Plain.

Additional evidence that supports the recognition of *Fusconaia apalachicola* as a distinct species is found in the zoogeography of aquatic organisms in the eastern Gulf drainages. There are several distinct and well documented breaks in east/west

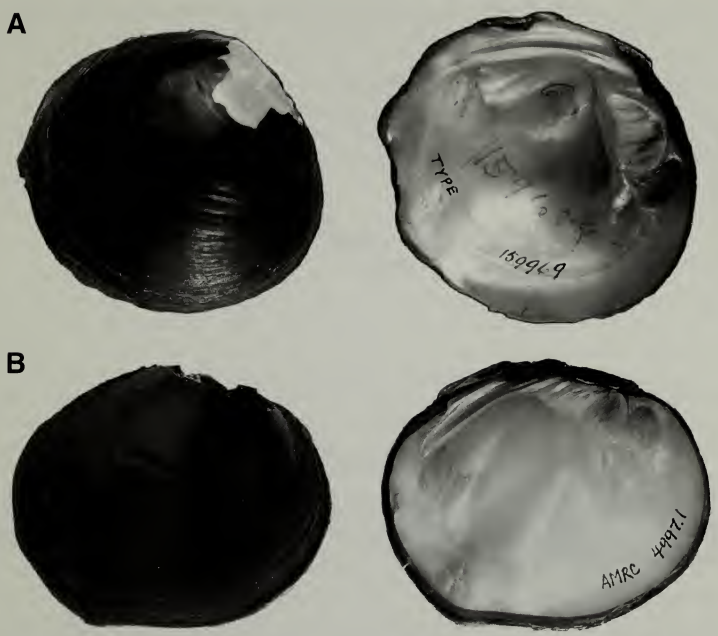

Figure 3. A) *Fusconaia rotulata*. Holotype, USNM 159969, length 46 mm. Escambia River, Escambia County, Florida. B. H. Wright. Photo by Jim Williams. B) *Fusconaia rotulata*. AMRC 4997.1, length 61 mm. Conecuh River, 1 mile above Alabama Highway 41, south of East Brewton, Escambia County, Alabama. 17 August 1996. Photo © by Richard Bryant.

distribution of aquatic species in the eastern Gulf drainages. One of the most pronounced breaks in distribution of aquatic fauna occurs between the west Florida rivers, the Escambia, Yellow, and Choctawhatchee, and the Apalachicola, Chattahoochee, and Flint rivers. This is reflected in the large number of endemic mussels and fishes in the two areas and the reduced number of species that the two areas share in common (Swift et al., 1986; Brim Box and Williams, in press; Clench and Turner, 1956).

Distribution: Based on the material available, the Apalachicola ebonyshell appears to have been restricted to the Apalachicola Basin (Figure 1). We currently have material from the Apalachicola River in Florida and Chattahoochee River on the Alabama and Georgia border in southeastern Alabama. We also examined two

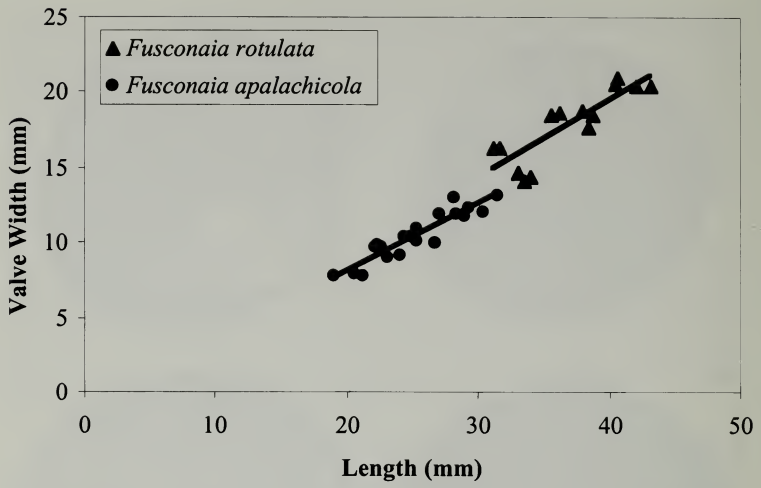

Figure 4. Relationship of valve width to length (distance from anterior margin of the anterior muscle scar to the anterior margin of the posterior muscle scar) in *Fusconaia rotulata* and *Fusconaia apalachicola*.

archaeological faunal collections housed at the Columbus Museum, Georgia. Of the two samples, one was from a site on the Chattahoochee River in east Alabama, the Abercrombie Site (1RU61), Russell County. The other site was the Cannon Site on the Flint River (9CP108), Crisp County, Georgia. These samples had similar species assemblages but did not contain *Fusconaia apalachicola*. We also examined one sample from an archaeological site (8WL81) in the Choctawhatchee River drainage, Walton County, west Florida, but no specimens of *F. apalachicola* or *F. rotulata* were present (Fradkin, 1995b).

The four archaeological sites, three in Florida and one in Alabama, that contained specimens of *Fusconaia apalachicola* range in age from A.D. 500 to 1350. The three Florida sites are located along the main channel of the upper reach of the Apalachicola River (Figure 1). Site 8LI76, Liberty County (Maymon et al., 1996), and the Sycamore Site (8GD13), Gadsden County (Milanich, 1974), are situated along the east side of the river. The Scholz Steam Plant Site (8JA104), Jackson County, is located on the west side of the river (Percy, 1976). All three are inland sites and were occupied during the middle or late Weeden Island culture period, ranging from approximately A.D. 500 to 1000. The Omussee Creek Site (1HO26) (Figure 1), Houston County, Alabama, is located on the lower Chattahoochee River and dates to the Rood phase of the Mississippian period, approximately A.D. 900 to 1350 (Schnell et al., 1981).

ETYMOLOGY: Derivation of the word Apalachicola is not clear. One interpretation is that Apalachicola is derived from the Hitchiti Indian words apalahchi = on the other side, and okli = people, referring to people who live on the other side of the river (Read, 1937). Another interpretation is from the Choctaw word Apelichi = ruling place, and Okla = people, meaning people of the ruling place (Boyd, 1956). We apply this name in reference to the species' restricted distribution to the Apalachicola Basin. Apalachicola ebonyshell is suggested for the common name for *Fusconaia apalachicola*.

DISCUSSION

Mussel collections from the Apalachicola Basin date from 1833, when T. A. Conrad traveled across the Chattahoochee and Flint rivers. He collected mussels from the Flint River but was unable to sample the Chattahoochee River (Wheeler, 1935). Between 1830 and 1870, Isaac Lea described more than 60 species from the Apalachicola Basin, of which only 10 are currently recognized as valid. In the early 1900s, H. H. Smith of the Alabama Museum of Natural History collected large numbers of mollusks from the Apalachicola Basin. In a comprehensive study of the Apalachicola Basin mussels, Brim Box and Williams (in press) examined most of the available museum collections and 350 samples collected between 1990 and 1997, but no *Fusconaia* were found. During the past 150 years, there has been considerable effort expended in the collection of mussels in the Apalachicola Basin. Many of these samples were collected prior to major alterations in the watershed. It appears that no individuals of *F. apalachicola* were ever encountered.

The causal factors and time of extinction of *Fusconaia apalachicola* are not known. The presence and abundance of this mussel in archaeological remains dated to A.D. 1350 suggests that it was most likely extant when the Europeans arrived in North America. If this assumption is correct, then it likely disappeared in response to environmental change associated with settlement and development of the Apalachicola Basin. Significant habitat alterations in the Apalachicola Basin were well underway in the early 1800s. Glenn (1911) reported that 60% of the uplands on the Chattahoochee River, between its headwaters near Gainesville, Georgia, downstream to Atlanta, had been cleared. Sediment from the cleared lands had filled the river channel to the point that many ferries on the Chattahoochee River could not operate during most of the year (Glenn, 1911). Logs cut along the Chattahoochee River were floated downstream to sawmills on an island at Columbus, Georgia, where they were cut into lumber and the sawdust and bark dumped in the river. Cotton mills in Columbus were also dumping waste, fibers, and metal based-dies into the river (Brim Box and Williams, in press).

One of the more common mussels in archaeological faunal samples in the Apalachicola and Chattahoochee rivers, *Elliptoideus sloatianus*, is known in the Chattahoochee River from only two individuals collected in the 1830s (Brim Box and Williams, in press). While *E. sloatianus* persisted in the Apalachicola and Flint rivers, its early extirpation from the Chattahoochee was most likely due to the pollution of the river in the 1800s.

Based on conchological characters, *Fusconaia apalachicola* appears to be most closely

related to *F. rotulata*, which is endemic to the Escambia River drainage in Escambia County, Alabama, and in Escambia and Santa Rosa counties, Florida. Wright (1899) described *Fusconaia rotulata* as a new species and placed it in the genus *Unio* based on a single specimen. Simpson (1900a) reexamined the type specimen and, based on the characters of this individual, assigned it to the genus *Obovaria*. Subsequent workers (Heard, 1979; Johnson, 1967a, 1967b, 1969; Simpson, 1900b, 1914; Turgeon et al., 1998) continued to recognize *rotulata* as a species of *Obovaria*. After examining the type and additional specimens of *rotulata* and comparing conchological characters (teeth, hinge plate, and deep umbo pocket) with other species of *Obovaria* and *Fusconaia*, Williams and Butler (1994) concluded that, based on conchological characters, *rotulata* was a species of *Fusconaia*, not *Obovaria*. *Fusconaia rotulata* most closely resembles *F. ebena*, which is widespread in the Mississippi Basin and along the Gulf coast eastward to the Alabama River system. The other two species of eastern Gulf drainage *Fusconaia*, *F. escambia* and *F. succissa*, are easily distinguished from *F. rotulata* by the presence of a well developed posterior ridge.

The habitat of *Fusconaia apalachicola* and *F. rotulata* appears to have been very similar. *Fusconaia rotulata* is confined to the main channel of the Escambia River in areas with moderate current and a mixture of sand and gravel substrates. Based on museum records and recent collections, both species also appear to have very restricted distributions, being limited to large rivers in the lower Coastal Plain ecoregion. The small number of *F. rotulata* located in museum collections along with those found in a recent survey of the main channel of the Escambia River indicate that it has been rare during the past 100 years. Until additional archaeological samples from the Apalachicola Basin are analyzed, it is not possible to assess the prehistoric rarity of *F. apalachicola*. In proportion to other unionids in archaeological samples where it was found, *F. apalachicola* appeared to be uncommon; however, this perception may be due to the small number of samples examined. The rarity of *F. rotulata* may be due in part to the difficulty of collecting mussels that occur in deeper waters of the main channel of a river.

While the extinction of *Fusconaia apalachicola* is significant, it also has serious implications for the future of *F. rotulata*. The extinction of *F. apalachicola* was most likely due to the alteration of its main channel riverine habitat. The abusive land use practices in the 1800s, during the development of the Chattahoochee and Flint river watersheds, resulted in drastically altered hydrology of these systems (Glenn, 1911; Brim Box and Williams, in press) which most likely extended downstream to the Apalachicola River. *Fusconaia rotulata*, like *F. apalachicola*, has a limited geographic distribution and is restricted to the main channel of the Escambia and Conecuh rivers. These factors, in combination with the current alteration of land, riparian, and stream habitats in the Escambia River watershed, make *F. rotulata* an at risk species with a high probability of extinction.

Mussel samples from the three Florida sites where *Fusconaia apalachicola* was found also contained the following 13 species: *Amblema neislerii*, *Elliptio crassidens*, *E. icterina*, *Elliptoideus sloatianus*, *Glebula rotundata*, *Lampsilis straminea claibornensis*, *L. teres*, *Medionidus penicillatus*, *Megalonaias nervosa*, *Pleurobema pyriforme*, *Quincuncina infucata*, *Villosa lienosa*, and *V. vibex*. Only five mussels, *Elliptio crassidens*, *E. icterina*, *Elliptoideus sloatianus*, *Pleurobema pyriforme*, and *Quincuncina infucata*, were present

in the sample from the mouth of Omussee Creek on the Chattahoochee River, Houston County, Alabama. In the Apalachicola Basin, these species typically occur in large creeks and rivers in a substrate of gravel, sand, clay, or mixture of sand and clay. *Fusconaia apalachicola* is the only species of unionid known to become extinct before it was discovered and described. Based on abundant archaeological samples from the southeastern United States, no other extinct species have been found which were undescribed.

Acknowledgments

We would like to thank the following individuals for their assistance in providing access to specimens and collections in their care: Dr. David Dickel, Bureau of Archaeological Research, Division of Historic Resources, Department of State, Tallahassee, Florida; Mr. Kurt Auffenberg, Dr. Fred Thompson, and Dr. Elizabeth Wing, Florida Museum of Natural History, Gainesville, Florida; Dr. Frank Schnell, Columbus Museum, Columbus, Georgia; Mr. Doug Shelton, Alabama Malacological Research Center Collection, Mobile, Alabama; Dr. Art Bogan, North Carolina State Museum of Natural Sciences, Raleigh, North Carolina; Dr. Paul Parmalee, Frank H. McClung Museum, University of Tennessee, Knoxville, Tennessee, and Kevin Cummings, Illinois Natural History Survey, Champaign, Illinois. We also appreciate the review and comments on an early draft of this manuscript by Drs. Bogan and Parmalee.

We would also like to thank Mr. Dick Bryant for the use of his photographs, Ms. Amy Benson for the preparation of the distribution map, and Ms. Sherry Bostick for her assistance in manuscript preparation.

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Volume 31, Number 2 25 March 2002

NEW SPECIES AND NEW RECORDS OF PSEUDOTHELPHUSID CRABS (CRUSTACEA: BRACHYURA) FROM COLOMBIA

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A REVIEW OF THE SPINYCHEEK SLEEPERS, GENUS ELEOTRIS (TELEOSTEI: ELEOTRIDAE), OF THE WESTERN HEMISPHERE, WITH COMPARISON TO THE WEST AFRICAN SPECIES

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TULANE STUDIES IN ZOOLOGY AND BOTANY
ISSN 0082-6782
Tulane University Museum of Natural History
Building A-3, Wild Boar Road
Belle Chasse, Louisiana 70037

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NEW SPECIES AND NEW RECORDS OF PSEUDOTHELPHUSID CRABS (CRUSTACEA: BRACHYURA) FROM COLOMBIA

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Abstract

The collections of freshwater crabs from Colombia deposited at the Tulane Natural History Museum contain representatives of 14 species. Three of them, *Hypolobocera noanamensis, Lindacatalina sinuensis* and *Moritschus altaquerensis*, are new species. Several taxa present noteworthy disjunctions. *Lindacatalina orientalis* (Pretzmann, 1968) and *L. sumacensis* Rodríguez and von Sternberg, 1998, display a trans-Andean distribution, with areas widely separated in Ecuador and Colombia. *Hypolobocera beieri* Pretzmann, 1968, and *H. lloroensis* Campos, 1989, are found in the Pacific and Atlantic slopes of the Andes. The new species *Lindacatalina sinuensis* comes from the Sinú River, which drains into the Atlantic, while other members of the genus are located more than 800 km away, in basins draining to the Amazon.

Introduction

The areas of distribution of most species of pseudothelphusid crabs usually cover continuous tracts along the watercourses. In the case of many Andean species, these areas are small, usually covering less than 100 km^2. Long-range specific distributions, particularly involving trans-basin disjunctions, are very rare. Among the few examples that could be found in the literature are *Hypolobocera bouvieri angulata* (Rathbun, 1915), from the Sierra Nevada de Santa Marta, Colombia, and the Sierra de Perijá, Venezuela (Rodríguez, 1982a), and two species from Ecuador, *Hypolobocera aequatorialis* (Ortmann, 1897) and *Lindacatalina orientalis* (Pretzmann, 1968), both with trans-Andean areas of dis-

Tulane Studies in Zoology and Botany 31:1-17, 2002.

tribution in the Pacific and Amazonian basins (Rodríguez and von Sternberg, 1998).

For more than 25 years, Dr. Alfred C. Smalley, from Tulane University, gathered an important collection of freshwater crabs from the Neotropics (Rodríguez and Fitzpatrick, 1996). Among the 14 species and subspecies from Colombia represented in this collection, three new species were discovered, one of them displaying a conspicuous generic disjunction between the Atlantic slopes of northern Colombia, the Pacific slopes of southern Colombia, and the Amazon basin of Ecuador. One species, previously known in the literature from localities in the Pacific slopes of the Andes, were found in the Atrato River that drains into the Atlantic, and two other display a trans-Andean distribution, with areas widely separated in Ecuador and southern Colombia.

In the present contribution we describe the three new species discovered and discuss the size of the areas of distribution of the Andean Pseudothelphusidae, in the light of the new data provided by the Smalley collection.

All the materials recorded are deposited in the Museum of Natural History of Tulane University, New Orleans (TU), the Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (ICN-MHN-CR) and the Museo de Biologia Marina, Universidad del Valle, Cali, Colombia, (MBMUV). Other abbreviations used are cl. for carapace length and cb. for carapace breadth.

Systematic Account

Family Pseudothelphusidae Rathbun, 1893
Subfamily Pseudothelphusinae Ortmann, 1893
Tribu Strengerianini Rodríguez, 1982a

Genus *Chaceus* Pretzmann, 1965
Chaceus pearsei (Rathbun, 1915)

Material Examined: 1 male, cl. 16.7 mm, cb. 25.9 mm, 1 soft-shelled female, 9 August 1965, road above Minca, 1,020 m alt., Cesar Department, Colombia, A. E. Smalley, TU 5388.

Genus *Phallangothelphusa* Pretzmann, 1965
Phallangothelphusa dispar (Zimmer, 1912)

Material Examined: 1 female, cl. 20.0 mm, cb. 34.0 mm, 1 August 1981, El Triunfo (4°33'N, 74°29'W), Cundinamarca Department, Colombia, TU 6304.

Genus *Strengeriana* Pretzmann, 1971
Strengeriana taironae Rodríguez and Campos, 1989

MATERIAL EXAMINED: 1 male, cl. 12.3 mm, cb. 21.6 mm, 1 juvenile female, cl. 6.0 mm, cb. 11.8 mm, 26 February 1964, San Lorenzo near Santa Marta, 2,700 m alt., Magdalena Department, Colombia, C.A. Velásquez and F. Medem, TU 4917.

Tribu HYPOLOBOCERINI Pretzmann, 1971

Genus *Hypolobocera* Ortmann, 1897
Hypolobocera beieri Pretzmann, 1968
Figs. 1J-K

MATERIAL EXAMINED: 2 males, cl. 16.0, 15.3 mm, cb. 25.0, 24.2 mm, 1 female, cl. 11.0, cb. 16.5 mm, 24 June 1965, Cauca River tributary of Meléndez River, 3 km upstream from Carmelo near Cali, Valle del Cauca Department, Colombia, A. E. Smalley and Zapata, TU 5381; 1 male juvenile with broken carapace, 2 October 1982, Alto Anchicaya, Valle del Cauca Department, Colombia, von Prahl, TU 6383; 1 female, cl. 18.5 mm, cb. 31.5 mm, 1 juvenile, cl. 10.5 mm, cb. 15.8 mm, 1 June 1965, Meléndez River, Valle del Cauca Department, Colombia, Moberly, TU 5459; 1 male, cl. 18.2 mm, cb. 28.4 mm, 6 August 1965, El Salto de Jorge, Anchicaya river, tributary of Dagua River, highway to Buenaventura, Valle del Cauca Department, Colombia, A. E. Smalley and Zapata, TU 5383; 1 male juvenile, cl. 11.2 mm, cb. 17.0 mm, 1 female, cl. 9.4 mm, cb. 14.6 mm, 30 June 1965, tributary of Meléndez River, 3.5 km upstream from Carmelo, about 14.5 km SE Cali, Valle del Cauca Department, Colombia, A. E. Smalley and Zapata, TU 5377; 7 males, cl. range 11.5 - 7.9 mm, cb. range 17.8 - 12.5 mm, 4 females, cl. range 8.6 - 9.8 mm, cb. range 12.6 - 14.5 mm, 3 juveniles, cl. 7.0, 6.5, 6.2 mm, cb. 10.5, 9.5, 8.0 mm, 14 July 1965, Quebrada de Nidios, forestry station near Pico de Loro and 1.5 km S Ponce, Valle del Cauca Department, Colombia, A. E. Smalley, Zapata and Adler, TU 5379; 3 males, cl. 13.5, 12.4, 9.2 mm, cb. 20.7, 19.1, 13.9 mm, 2 female, cl. 14.9, 11.4 mm, cb. 22.3, 16.9 mm, 1 June 1965, tributary of Anchicaya River, 9 km west of El Salado, Valle del Cauca Department, Colombia, A. E. Smalley and Zapata, TU 5376; 1 male juvenile, cl. 12.7 mm, cb. 20.4 mm, 3 ovigerous females, cl. 21.8, 19.1, 18.9 mm, cb. 38.8, 31.8, 30.2 mm, 3 females, cl. 18.1, 16.5, 16.2 mm, cb. 30.2, 26.5, 25.9 mm, 1 juvenile with broken carapace, 15 March 1980, left margin of Mazamorra River, tributary of Guachicono River, 1,400 m alt., Valle del Cauca Department, Colombia, Matidnell, TU Acc N° 94-100; 3 males, cl. 18.5, 18.4, 15.4 mm, cb. 29.9, 29.7, 24.5 mm, 3 females, cl. 21.4, 19.9. 10.4 mm, cb. 36.1, 31.5, 16.2 mm, 5 January 1967, mountain stream near Pichinde, Valle del Cauca Department, Colombia, Dale Little, TU 5588; 2 males, cl. 14.6, 11.8 mm, cb. 22.9, 17.8 mm,

17 June 1965, small tributary of Paila River, 4.3 km E Cornito, Cauca River, Valle del Cauca Department, Colombia, A. E. Smalley, TU 5380.

Hypolobocera noanamensis, new species
Figs. 1A-H

HOLOTYPE: Adult male, cl. 50.9 mm, cb. 80.3 mm, 8 August 1969, Noanamá, San Juan River (4°42'N, 26°56'W), Chocó Department, Colombia, Dale Little, TU 6191.

PARATYPE: 1 mature female, cl. 53.9 mm, cb. 80.3 mm, collected with holotype, TU 5337.

DIAGNOSIS: First male gonopods with caudal ridge strong, fusiform, thickened at middle, ending in narrow ridge beyond lateral lobe, crossed by thin transverse lines; lateral lobe small, subtriangular, with distal angle rounded, projected, proximal border traverse or slightly convex, placed transversely in relation to axis of appendage; cephalic surface with tuberculated crest. Apex funnel-form, distal angle not projected, outline of apex oval in distal view, with meso-cephalic border rounded, expanded, prominent papilla near cephalic border, spermatic channel with spiny ridge on meso-caudal side and flat, wide papilla on caudo-lateral side.

DESCRIPTION OF HOLOTYPE: Carapace 1.58 times as wide as long, surface smooth, regions strongly marked by deep depressions; cervical grooves deep and straight becoming indistinct toward margins of carapace. Anterolateral margins with deep V-shaped notch behind outer orbital angle, devoid of papillae; margin posterior to cervical groove with approximately six wide obsolescent lobes, rest of margin with eight wide subtriangular teeth. Postfrontal lobes rounded, forming two prominent swellings; median groove very wide between postfrontal lobes, indistinct in front of postfrontal lobes, making deep V-shaped incision on upper margin of front. Surface of carapace in front of postfrontal lobes inclined anteriorly and towards middle. Upper margin of front bilobed in dorsal view, angulated, devoid of defined papillae; lower margin strongly sinuous in frontal view and conspicuously thickened; space between both margins very narrow.

Third maxilliped with lateral border of merus of endognath straight, ending distally in rounded lobe and deep depression; exognath 0.3 length of ischium of endognath. Orifice of efferent branchial channel open. Chelipeds moderately unequal, finger of larger one (right) with small gap when closed, palm slightly swollen; rows of small black points on external and upper surfaces of mobile finger and external surface of fixed finger, scattered small tubercles on internal lower surface of palm. Carpus with prominent spine on internal upper margin; internal upper margin of merus with row of teeth, row of smaller teeth on exter-

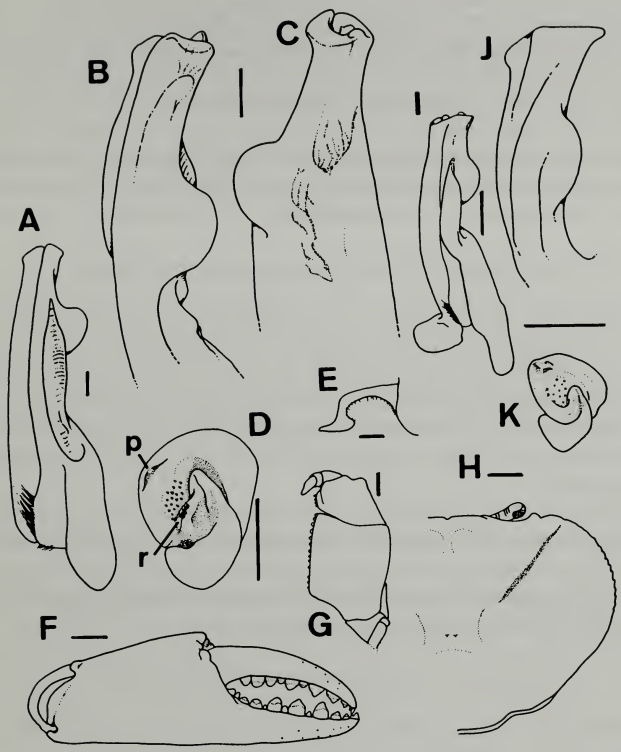

Figure 1. *Hypolobocera noanamensis,* new species, male holotype from Noanamá, San Juan River, Chocó Department, Colombia (TU 6191), A-D, first left gonopod: A, caudal view; B, lateral view; C, cephalic view; D, apex, distal view; E, aperture of efferent channel; F, larger chela, right; G, left third maxilliped; H, dorsal view of right side of carapace; *Hypolobocera beieri* Pretzmann, 1968, male cb. 24.2 mm, from Cauca River, near Cali, Colombia (TU 5381), first left gonopod: I, caudal view; J, lateral view; K, apex, distal view; r, spiny ridge; p, papilla. Scales A-D = 1 mm, E, G = 3 mm, F,H = 1 cm, I, J, K = 1 mm.

nal margin and prominent tubercles on lower margin.

First male gonopods slender, arched cephalically; caudal ridge strong, fusiform, thickened at middle, ending in narrow ridge beyond lateral lobe, crossed by thin transverse lines; lateral lobe small, subtriangular, with distal angle rounded, projected, proximal border traverse or slightly convex, placed transversely in relation to axis of appendage; cephalic surface with tuberculated crest. Apex funnel-form, with distal angle not projected in lateral view, outline of apex oval in distal view, with meso-cephalic border rounded, expanded, prominent papilla near cephalic border, spermatic channel with spiny ridge on meso-caudal side and flat, wide papilla on caudo-lateral side.

Remarks: The first gonopods of *Hypolobocera noanamensis* resemble those of *H. bouvieri rotundilobata* Rodríguez, 1994, and H. *beieri*, but it can be distinguished from both by the spiny ridge on the caudal side of the spermatic channel (Fig. 1D, r), the shape and relative development of the lateral lobe, and the outline of the apex. In *H. beieri* the apex forms a beak-like projection on the cephalic side (Fig. 1J) and the apical outline in distal view (Fig. 1K) has the meso-cephalic border transverse, not rounded and expanded (Fig. 1D). In H. *bouvieri rotundilobata* the apical outline in distal view has the meso-cephalic border subtriangular, projected.

Size: This is a large species. The mature female paratype has a cb. of 80.3 mm

Etymology: The species is named after the Noanamá locality in the San Juan River, Colombia, where the species was collected.

Hypolobocera bouvieri bouvieri (Rathbun, 1898)

Material Examined: 1 male, cl. 25.6 mm, cb. 40.4 mm, 22 September 1982, Finca Villa Christina, Municipio Santardercito, Cundinamarca Department, Colombia, von Prahl, TU 6382; 1 male, cl. 35.0 mm, cb. 57.5 mm, 7 November 1981, La Mesa, 1,500 m alt., Cundinamarca Department, Colombia, TU 6355; 2 males, cl. 21.8, 16.4 mm, cb. 32.1, 24.4 mm, 21 April 1982, Sasaima, 1,500 m alt. (4°58'N, 74°26'W), Cundinamarca Department, Colombia, von Prahl, TU 6376; 1 male, cl. 52.4 mm, cb. 89.6 mm, 28 November 1981, Doima River, Municipio Doima, Tolima Department, Magdalena basin, Colombia, TU Acc N° 94-100.

Hypolobocera bouvieri angulata (Rathbun, 1915)

Material Examined: 1 immature male, cl. 20.0 mm, cb. 30.2 mm, 9 August 1965, highway from Santa Marta to Riohacha, 10 km from Bonda, Magdalena Department, Colombia, A. E. Smalley, TU 5382.

Hypolobocera gorgonensis von Prahl, 1983

MATERIAL EXAMINED: 1 male, cl. 50.6 mm, cb. 83.3 mm, 22 August 1980, Gorgona Island, Valle del Cauca Department, Colombia, von Prahl, TU 6303.

Hypolobocera lloroensis Campos, 1989

MATERIAL EXAMINED: 1 male, cl. 24.4 mm, cb. 40.0 mm, 2 females, cl. 26.3, 13.8 mm, cb. 43.9, 21.8 mm, 8 August 1969, Istmina, San Juan River, Chocó Department, Colombia, Dale Little, TU 6193.

Hypolobocera merenbergiensis von Prahl and Giraldo, 1985

MATERIAL EXAMINED: 1 male holotype, cl. 13.1 mm, cb. 20.1 mm, 3 females, cl. 14.0, 13.4, 11.5 mm, cb. 23.4, 21.8, 18.2 mm, MBMUV-82051, 1 female paratype, cl. 14.2 mm, cb. 22.5 mm, ICN-MHN-CR 0541, 2 males, cl. 12.3, 10.5 mm, cb. 18.8, 16.5 mm, TU 6369, 8 April 1982, Finca Merenberg, 2,300 m alt., Cordillera Central, Huila Department, Colombia, H. von Prahl and J. Giraldo.

REMARKS: We list above the seven extant specimens from the original collection deposited in several museums. Von Prahl & Giraldo (1984) gave a list of six specimens with their respective measurements and, separately, they designated the holotype and four paratypes, without indication of their sizes. They did not recorded the sex of the specimens measured, but gave the length of the gonopod for one of them (cb. 19.8 mm). This is the only male in the collections of the MBMUV and consequently must be considered as the male holotype designated by von Prahl & Giraldo (1984). They designated as male paratype a specimen deposited at TU. Since there are two male specimens at TU, this probably refers to the largest one.

Von Prahl & Giraldo (1984) recorded three female paratypes, one of them deposited at the ICN-MHN-CR, and two at the MBMUV. They stated that these last were marked as numbers 48 and 49, but we could not find the respective labels, and furthermore, there are three females at the MBMUV instead of the two implied in the designation of the paratypes. Consequently, we cannot determine to which of the females in the MBMUV corresponds the status of paratypes. Our measurements of the cb. show slight discrepancies with the measurements given by Von Prahl & Giraldo (1985). The discrepancies are even larger for cl. measurements.

Lindacatalina Pretzmann, 1977

Lindacatalina sinuensis, new species

Figs. 2A-H

HOLOTYPE: Adult male, cl. 10.0 mm, cb. 15.6 mm, 3 August 1965, 80 km up Sinú River, from Tierra Alta, small waterfall tributary of Sinú River, Córdoba Department, Colombia, Kraig Adler, TU 5337.

PARATYPE: 1 ovigerous female, cl. 14.9 mm, cb. 23.8 mm, collected with holotype, TU 5337.

DIAGNOSIS: First male gonopods with lateral margin divided longitudinally into two distinct halves, one caudal, small, rounded, another lateral, larger, circular in outline, covered by stout spines. Apex in distal view elongated in mesolateral axis, oval, with flat papilla over field of spines.

DESCRIPTION OF HOLOTYPE: Carapace 1.56 times as wide as long, surface covered with small papillae not visible to naked eye, regions of carapace clearly defined; cervical grooves shallow and straight, becoming indistinct toward margins of carapace. Anterolateral margins with wide shallow notch behind outer orbital angle, notch with papillae on margin; not meeting anteroexternal orbital angle, continuing above orbital margin; posterior to cervical groove with approximately 15 small teeth. Postfrontal lobes small, forming two slight swellings placed transversely in relation to middle axis of carapace; median groove shallow, ill defined. Surface of carapace in front of postfrontal lobes inclined anteriorly. Upper margin of front bilobed in dorsal view and bearing row of ill defined papillae; lower margin strongly sinuous in frontal view and conspicuously thickened; space between both margins moderately high.

Third maxilliped with lateral border of merus of endognath forming regular curve, with deep depression on distal part of external margin. Exognath of third maxilliped 0.3 length of ischium of endognath. Orifice of efferent branchial channel open. Chelipeds unequal, finger of larger one with small gap when closed, palm slightly swollen. Carpus with prominent spine on internal upper margin; internal upper margin of merus with rows of teeth.

First male gonopods arched cephalically, caudal ridge prominent, with few transverse wrinkles at middle section. Lateral margin divided longitudinally into two distinct halves, one caudal, small, rounded, formed by distal expansion of caudal ridge, and another lateral, larger, circular in outline, covered by stout spines. Apex in distal view elongated in mesolateral axis, oval, with flat papilla over field of spines.

REMARKS: We are tentatively placing this species in the genus *Lindacatalina* due to the presence of two parallel lateral lobes, one of them densely covered with

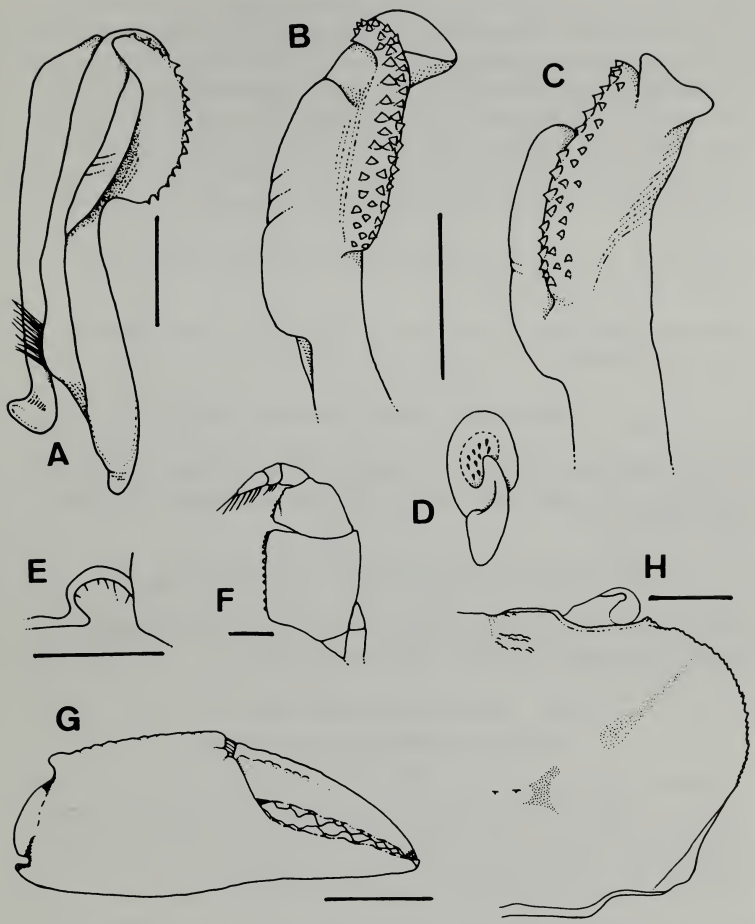

Figure 2. *Lindacatalina sinuensis*, new species, male holotype from Sinú River, Córdoba Department, Colombia (TU 5337), A-D, first left gonopod: A, caudal view; B, lateral view; C, latero-cephalic view; D, apex, distal view; E, aperture of efferent channel; F, left third maxilliped; G, larger chela, right; H, dorsal view of right side of carapace. Scales A-F = 1 mm, G-H = 3 mm.

spines. However, the length of exognath in *Lindacatalina* is usually more than 0.45 times the length of the ischium of endognath, and the spines over the lateral lobe of the gonopods are similar to those over the field of spines (Rodríguez and von Sternberg, 1998), whereas in the new species the proportions of the above structure is 0.3, and the spines over the lateral lobe are larger and stronger than those over the field of spines. *Lindacatalina sinuensis* resembles *L. sumacensis* in the caudal ridge covered by minute transverse wrinkles, but the latero-cephalic half of the lateral lobe is not expanded distally as is the case in *L.sumacensis*.

SIZE: This is a relatively small species for the family. The ovigerous female paratyper has a cb. of 28.3 mm.

ETYMOLOGY: The species is named after the Sinú River, in whose basin the species was collected.

Lindacatalina orientalis (Pretzmann, 1968)

MATERIAL EXAMINED: 1 male, cl. 15.7 mm, cb. 24.7 mm, 1 female, cl. 12.5 mm, cb. 18.8 mm, 24 October 1969, Sibundoy, Putumayo Department, Colombia, Dale Little, TU 6192.

Lindacatalina sumacensis Rodríguez and von Sternberg, 1998

MATERIAL EXAMINED: 1 male, 19.6 mm, cb. 31.2 mm, 7 July 1969, Mocoa, Putumayo Department, Colombia, Dale Little, TU 6194.

Moritschus Pretzmann, 1965
Moritschus altaquerensis, new species
Figs. 3A-H

HOLOTYPE: 1 male, cl.16.0 mm, cb.26.7 mm, 29 July 1999, Vereda El Mirador, Corregimiento Altaquer, 1,200 m alt. (1°13'49"N, 78°02'18" W), Municipio Barbacoas, Nariño Department, M. R. Campos, ICN-MHN-CR 1769.

PARATYPE: 9 males, cl. range 13.5 - 10.6 mm, cb. range 22.1 - 16.7 mm, 7 females, cl. range 15.0 - 10.8 mm, cb. range 24.0 - 17.1 mm, collected with holotype, ICN-MHN-CR 1770.

ADDITIONAL MATERIAL EXAMINED: 5 males, cl. range 12.5 - 10.0 mm, cb. range 20.2 - 16.0 mm, 6 females, cl. range 15.2 - 11.8 mm, cb. range 24.4 - 18.8 mm, 30 July 1999, Vereda Ospina, 1,300 m alt. (1°13'18"N, 78°02'10"W), Municipio Ricaurte, Nariño Department, Colombia, M. R. Campos, ICN-MHN-CR 1771; 6

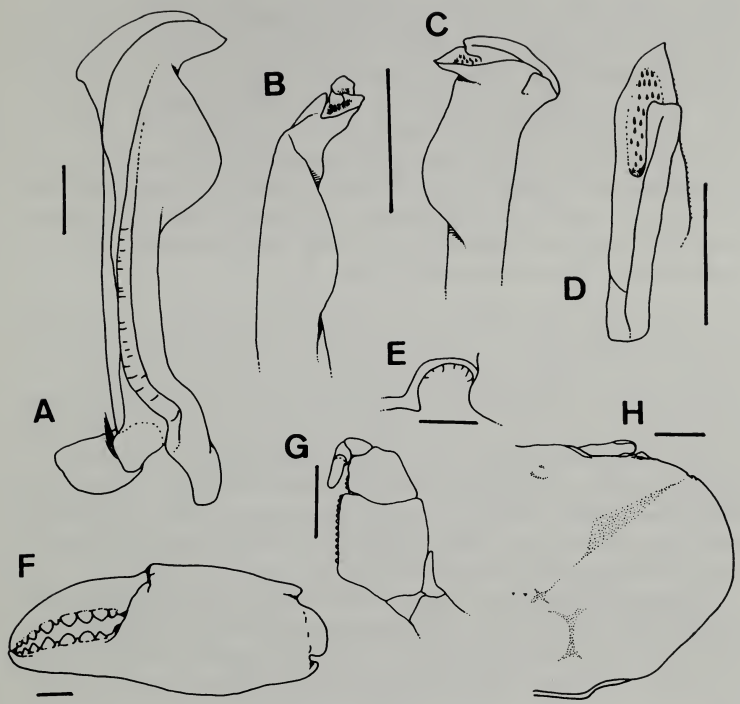

Figure 3. *Moritschus altaquerensis*, new species, male holotype from Altaquer, Municipio Barbacoas, Nariño Department, Colombia (ICN-MHN-CR 1769), A-D, first left gonopod: A, caudal view; B, lateral view; C, cephalic view; D, apex, distal view; E, aperture of efferent channel; F, larger chela, left; G, left third maxilliped; H, dorsal view of right side of carapace. Scales A-E = 1 mm, F-H = 3 mm.

males, cl. range 15.2 - 12.6 mm, cb. range 25.1 - 19.4 mm, 1 female, cl. 13.8 mm, cb. 22.1 mm, 30 July 1999, stream affluent of Nembí River, Vereda Ospina, 1,200 m alt. (1°13'23"N, 78°02'15"W), Municipio Ricaurte, Nariño Department, Colombia, M. R. Campos, ICN-MHN-CR 1772; 1 male, cl. 15.3 mm, cb. 25.4 mm, 1 female, cl. 14.6 mm, cb. 23.5 mm, 11 July 1969, stream near Altaquer, Nariño Department, Dale Little, TU 6178.

DIAGNOSIS: First male gonopod with lateral lobe prominent, forming winged subtriangular expansion, extending from middle of appendage to below apex, caudal end produced in short beak. Apex in distal view strongly elongated along mesolateral axis, arched, with minute spines on caudal margin; elongated process over field of spines with two rudimentary papillae.

DESCRIPTION OF HOLOTYPE: Carapace 1.66 times as wide as long, dorsal surface smooth, limits between regions well marked; cervical groove shallow and straight, wide posteriorly, narrow anteriorly, reaching margin of carapace. Anterolateral margin with shallow notch behind orbit, not reaching outer orbital angle, shallow notch at level of cervical groove, anterolateral border with about 12 papillae. Postfrontal lobes small, oval, indicated anteriorly by transverse slightly depression, median groove obsolete. Surface of carapace in front of postfrontal lobes inclined anteriorly. Superior frontal border smooth, not bilobed in dorsal view, inferior border visible in dorsal view, strongly sinuous in frontal view and conspicuously thickened, front narrow.

Chelipeds strongly unequal, palm of larger one (left) inflated, fingers gaping, movable finger slightly arched. Third maxilliped with merus of endognath regularly curved, with shallow depression on distal part of external margin; exognath 0.36 length of ischium of third maxilliped. Orifice of efferent branchial channel open.

First male gonopod slender, arched laterally; caudal ridge elongated longitudinally; lateral lobe prominent, forming winged subtriangular expansion, extending from middle of appendage to below apex, caudal end produced in short beak; apex in distal view strongly elongated along mesolateral axis, arched, with minute spines on caudal margin; elongated process over field of spines with two rudimentary papillae.

COLOR: The holotype is dark brown with paler brown specks on the dorsal side of the carapace. The walking legs are brown dorsally, and light brown ventrally. The chelae are brown dorsally, and buffy-brown ventrally. The ventral surface of the carapace is buffy-brown.

HABITAT: The specimens were collected in shady, moist banks of springs and small streams. They were found in soft mud, under rocks, or in borrows.

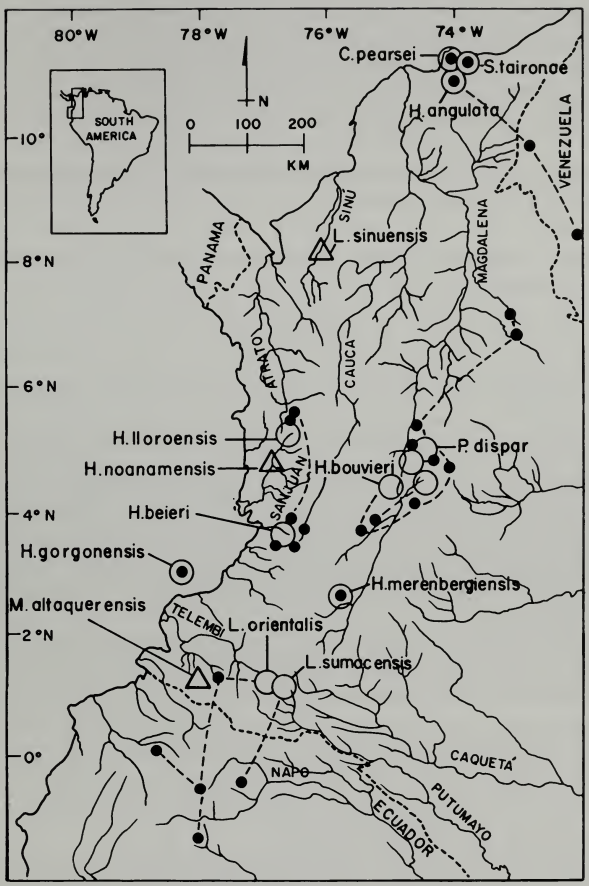

Figure 4. Geographic distribution of Colombian species of Pseudothelphusidae. Triangles, new species; open circles, new records; dots, previous records.

REMARKS: The first gonopods of the new species resemble those of *Moritschus ecuadorensis*, but its lateral margin forms a well defined subtriangular expansion, whereas in *M. ecuadorensis* it stretches out progressively towards the apex. Furthermore the elongated process over the field of spines in *M. ecuadorensis* presents a notch between two rudimentary papillae, while in *M. altaquerensis* the apex of this process is continuous.

SIZE: This is a relatively small species for the family. A mature female has a cb. of 24.4 mm (ICN-MHN-CR 1771.

ETYMOLOGY: The specific epithet is derived from the locality's name where the species was collected.

BIOGEOGRAPHY

The records given above shed new light on the sizes of the areas of distribution of several Colombian species. The smallest area is that of *Hypolobocera gorgonensis*, an insular species restricted to Gorgona Island. The total surface of this island is only 15 km^2. *Chaceus pearsei* and *Strengeriana tayronae* are restricted to localities on the north and western slopes of the Sierra Nevada de Santa Marta. Our material of these three species come from the type localities, as well as that of *Hypolobocera bouvieri angulata*, but this last species posses a very large area of distribution which extends to the Sierra de Perijá and the Cordillera de Mérida in Venezuela (Fig. 4).

Hypolobocera bouvieri bouvieri has a very extensive distribution on the slopes of the Central and Eastern Cordilleras draining to the Magdalena River. Our specimens are nested within this area of distribution, towards the southern portion of its range. Our specimens of *Phallangothelphusa dispar* are also nested within the known area of distribution. The distribution area of this species overlaps, in the southern portion with that of *H. bouvieri bouvieri*. *Hypolobocera merenbergiensis* is known only from a single locality in the Cordillera Central, in the upper reaches of the Magdalena River.

The only previous record of *Hypolobocera lloroensis* is from the headwaters of the Atrato River, which flows northwards into the Gulf of Uraba, on the Atlantic coast. Our material comes from a region that, notwithstanding its proximity to the type locality, is situated on the basin on the San Juan River, which flows southwards to the Pacific coast of Colombia. This phenomenon is possibly due to intermittent communication of both basins during seasonal flooding in areas below 100 m of altitude. A similar phenomenon has been recorded for the Orinoco, Amazon, and the Atlantic rivers of the Guianas (Rodríguez, 1982b).

Hypolobocera beieri displays an interesting trans-Andean distribution. Numerous specimens of *H. beieri* present in the Tulane Collection come from the

main area of distribution of the species, in the upper reaches of the Cauca River, which drains into the Atlantic, but others were collected in the basin of the Anchicaya River, in the Valle del Cauca Department, that drains into the Pacific. Rodríguez (1994) also gives an isolated record of this species from the upper reaches of the San Juan River, near the type locality of another *Hypolobocera, H. bouvieri rotundilobata* Rodríguez, 1994. In the same San Juan River basin, towards its middle course, was collected *Hypolobocera noanamensis*.

Of special interest are the distribution areas of those Colombian species related to taxa distributed in the Ecuadorian Andes (Rodríguez and von Sternberg, 1998). The presence of *Lindacatalina orientalis* in Colombia has already been recorded by von Prahl (1988). The range of this species in Ecuador covers the basins of rivers draining both to the Amazon basin, through the Napo and Pastaza rivers, and to the Pacific through the Esmeraldas River. The present record follows the same pattern of trans-Andean distribution in southern Colombia, through the Putumayo and Telembi rivers, respectively. The record of *L. sumacensis* also extends the range of the species to Colombia, but in this case, within the Amazon basin.

The new species *Moritschus altaquerensis* belongs to a genus present in Ecuador and the southern Department of Nariño in Colombia. The only localities known for *Moritschus altaquerensis* are in the Telembi River (affluent of Patia River), less than 30 km from the type locality of *M. narinnensis* Campos and Rodriguez, 1988, and on the same river basin. The record of *Lindacatalina orientalis* given by von Prahl (1988) also comes from this river. Notwithstanding the close geographical proximity of *Moritschus altaquerensis* and *M. narinnensis*, the former species is more closely related in the morphology of its gonopod to *M. ecuadorensis* (Rathbun, 1897), a species restricted to the upper reaches of the Esmeraldas River in Ecuador, which is the next large river to the south of the Patia River, than to *M. narinnensis*.

Noteworthy is the disjunction of *Lindacatalina sinuensis* in regard to the rest of the species in the genus. The species of *Lindacatalina* are restricted to a sector of the eastern slope of the Ecuadorian Andes that drains to the Amazon basin (Rodríguez and von Sternberg, 1998), with the exception of *Lindacatalina orientalis* discussed above. The area of *L. sinuensis* is restricted to the Sinú River that drains into the Atlantic at the northernmost corner of Colombia, at a distance of more than 800 km from the main distribution area of the genus.

Acknowledgements

We express our thanks to Drs. Henry L. Bart, Jr., and Dr. Joseph F. Fitzpatrick, Jr. for entrusting the curation of this valuable collection to the senior author, and to Mr. Mike Taylor for his untiring help with the handling of the material.

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A REVIEW OF THE SPINYCHEEK SLEEPERS, GENUS *ELEOTRIS* (TELEOSTEI: ELEOTRIDAE), OF THE WESTERN HEMISPHERE, WITH COMPARISON TO THE WEST AFRICAN SPECIES

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Abstract

Species of the genus *Eleotris* from the eastern Pacific and western Atlantic are reviewed. Three species are recognized from the eastern Pacific region. The wide-ranging *Eleotris picta* Kner, *Eleotris tubularis* Heller and Snodgrass (endemic to Cocos Island), and *Eleotris tecta* Bussing (limited to Costa Rica, Panama and Colombia) are distinguishable by scale counts (size), cephalic neuromast features and morphology of the urogenital papilla. Three western Atlantic species are recognized. *Eleotris pisonis* (Gmelin) is a continental South American species ranging from southern Brazil to the Orinoco River delta in eastern Venezuela. A second primarily continental species, *E. amblyopsis* (Cope), is distributed from Brazil through the Caribbean basin and Gulf of Mexico to North Carolina. *Eleotris perniger* (Cope), largely Caribbean in distribution, is the prevalent species in the Antilles and Quintana Roo, but is also sympatric with *E. amblyopsis* in Central America. The three western Atlantic species differ in scale counts and cephalic neuromast patterns. *Eleotris daganensis* Steindachner of West Africa is morphologically indistinguishable from *E. amblyopsis*. Lacking evidence of connectivity between eastern Atlantic populations of *E. daganensis* and western Atlantic populations of *E. amblyopsis*, the species are not synonymized. *Eleotris annobonensis* Blanc, Cadenat and Stauch is similar to *E. perniger* and North American populations of *Eleotris amblyopsis*. The remaining three West African species of *Eleotris* are most similar to *E. picta* of the eastern Pacific. *Eleotris* and *Erotelis* are recognized as distinct genera.

Tulane Studies in Zoology and Botany 31:19-63, 2002.

Introduction

Spinycheek sleepers in the genus *Eleotris* are sit-and-wait predators characterized by a distinctive eleotrid morphology - moderately blunt large head, torpedo-like body form, broad, rounded caudal fin and prominent lower jaw (Fig. 1). In the tropics and subtropics, they are a common element in estuaries, insular freshwater streams and small continental streams with poorly developed freshwater ichthyofaunas. Although they are not important as food fishes in most places, spinycheek sleepers are likely an important component of these subtropical and tropical ecosystems, both as predators and, in the larval stage, as a food source (e.g. Nordlie, 1979, 1981; Perrone and Vieira, 1990, 1991). Despite the growing interest in their ecological roles in freshwater and estuarine communities, little attention has been given to the systematics of *Eleotris* species beyond the description of new species. The lack of significant interest is likely the synergistic result of the cosmopolitan distribution of the genus, a plethora of nominal species, few diagnostic characters with which to work and a confusing amount of state variation for those characters.

When it was extricated from *Gobius* 200 years ago, species included in the genus *Eleotris* were distinguished in that they lacked a cup-like base formed by joined pelvic fins, although the pelvic fins were described as connected by membranes (Bloch and Schneider, 1801). Through time the genus came to be identified with gobioid species with separate pelvic fins; species characterized by that feature were routinely tossed into the *Eleotris* bin throughout the 1800's and early 1900's (more than 200 species [Eschmeyer, 1998]). Although most of these species have been removed in turn to other genera, and in some cases families, the genus has never been revised or reviewed in its entirety and a number of nominal taxa remain for which validity has never been tested. Only two regional reviews have been accomplished. Akihito (1967) examined species from Japan and compared them to several other Indo-Pacific species. His study was particularly important in demonstrating the significance of the free neuromast patterns on the head for diagnosing species. More recently, Miller (1998) reviewed species from the eastern Atlantic. As did Akihito, he found cephalic free neuromast patterns and differences in squamation the most useful characters in separating species. Miller also offered what he termed a phenetic diagnosis of the genus based on the antrorse spine on the preoperculum, axial osteology and features of the cephalic lateralis system. He proposed that the genus *Erotelis* was a junior synonym of *Eleotris* as the former's two included species shared these diagnostic features.

This paper reports the results of a review of *Eleotris* species from the Western Hemisphere, the eastern Pacific and western Atlantic basins. Species are compared to West African *Eleotris* and a key is provided to the species of the

Figure 1. *Eleotris amblyopsis*, from Tortuguero, Costa Rica, NLU 69723.

western Atlantic and eastern Pacific oceans. *Eleotris* and *Erotelis* are distinguished and their separate recognition is recommended.

Methods

Meristic and mensural characters and procedures follow Hubbs and Lagler (1958), except for the following: preanal length, postanal length, head width at the preopercle, length of the urogenital papilla, body width at pectoral fin base, and body width at second dorsal fin origin. Preanal length is the least distance from the vent to the tip of the snout, and postanal length is the least distance from the vent to the hypural of the caudal peduncle. Head width is the greatest lateral distance through the fish at the preopercle. Urogenital papilla length was measured from the vent to the distal tip of the papilla. Body widths are the greatest distance through the body at the bases of the left and right pectoral fins, and the greatest distance through the body at the origin of the second dorsal fin. Head length, head width at preopercle, pre-dorsal length, nape height, preanal length, postanal length, caudal peduncle length, body width at pectoral fin base, body width at second dorsal fin origin, urogenital papilla length, pectoral fin length, pelvic fin length, and caudal fin length are reported as proportions of standard length (SL). Interorbital width, upper jaw length, orbit length, and snout length are reported as proportions of head length (HL). First dorsal fin pterygiophore insertion pattern formulas are as given in Birdsong et al. (1988). Meristic information is reported as mode (range).

Principal component analyses were used to separately investigate morphological and meristic variation among species. Principal component scores derived from untransformed morphological variables were regressed against standard length. To remove size as a factor in the analyses, residual values for each specimen were then used in the scatter plots. Preliminary analysis disclosed no sexual dimorphism for morphological features other than urogenital papilla form, which was not included in the analysis. Males and females were pooled in subse-

quent analyses. Samples of the wide-ranging species *Eleotris amblyopsis* and *E. picta* were studied for geographic variation. For these analyses, *Eleotris picta* samples were subdivided into roughly equal latitudinal regions because there are no obvious geographic barriers or restrictions to movement throughout its range. *Eleotris amblyopsis* samples were subdivided into natural geographic units based upon regional current patterns, land mass distributions and distribution patterns observed for other gobioid fishes in the western Atlantic (e.g. Pezold and Grady, 1989).

Cephalic neuromast distribution patterns and urogenital papilla anatomy were examined and illustrated using a dissecting microscope and camera lucida. Cephalic neuromast patterns are described using terminology developed by Sanzo (1911) with modifications employed by Miller and Wongrat (1991). Transverse suborbital rows are designated with Arabic numbers and major horizontal rows on the cheek are indicated with the letters *b* and *d*. To simplify references to the particular transverse suborbital rows crossing row *d*, a formula of row numbers separated by periods is used. For example, if rows 2, 3 and 4 cross row *d*, this condition is represented by the formula "2.3.4." Similarly, the notation "2.4" indicates rows 2 and 4 cross *d*. Some species had incompletely formed rows, termed "segments." To be considered a "row" instead of a "segment," a line of papillae would have to reach at least half the distance between the eye and horizontal row *d*. Transverse opercular rows are labeled *ot* and *ot'*. Upper and lower longitudinal rows on the operculum are labeled *os* and *oi*, respectively (Fig.2).

Decisions of species limits were rooted in the Evolutionary Species Concept (Wiley and Mayden, 2000). Operational applications differed for sympatric and allopatric populations. Reproductive isolation was inferred from concordant patterns of variation of at least two morphological characters in sympatric population samples (Brown and Wilson, 1952; Grady and Quattro, 2000). For species determinations of allopatric population samples, the degree of morphological differentiation between samples was compared to that observed among sympatric samples. In the latter case, the possibility for gene flow through dispersion or dispersal, and probable length of separation were also considered.

Museum acronyms follow Leviton et al., 1985 and Leviton and Gibbs, 1988, except where noted in the list of materials examined.

Results

Eastern Pacific. Three species of *Eleotris* are easily distinguished in the eastern Pacific basin using meristic features, cephalic neuromast patterns, urogenital papillae and pigmentation. Morphological variation was largely uninformative within or among species with the exception of the urogenital papilla (Table 1). Although some differences among species appeared in the simple examination of relative proportions presented in Table1, no significant interspecific distinctions

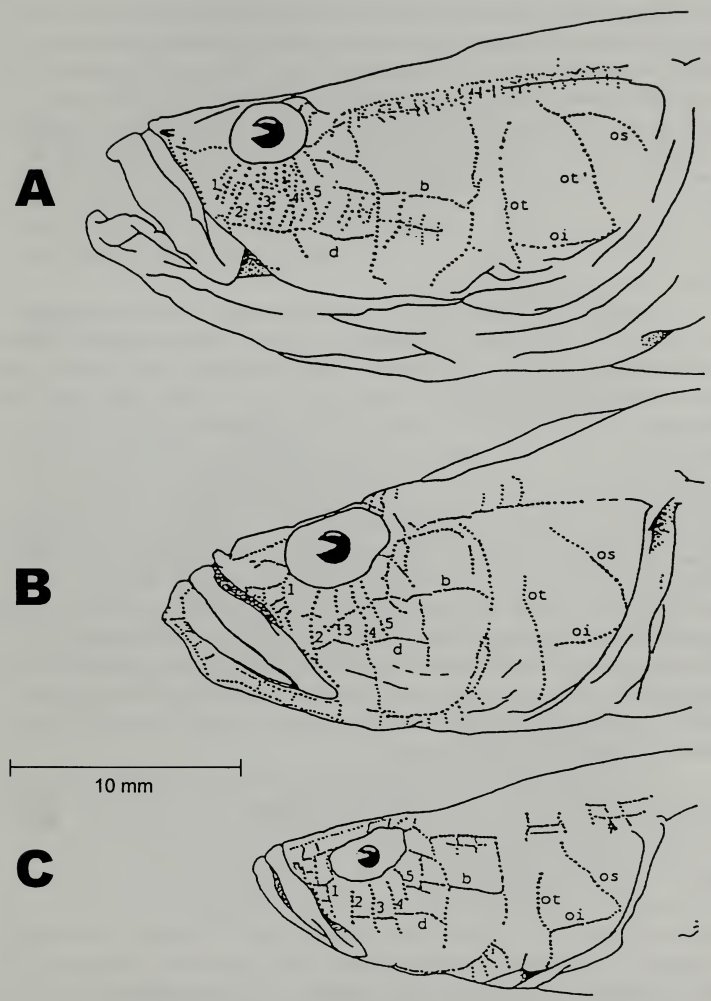

Figure 2. Cephalic free neuromast patterns of eastern Pacific *Eleotris* species. a) *Eleotris picta* b) *Eleotris tubularis* c) *Eleotris tecta.*

were retained in the multivariate analysis after principal component scores were corrected for size correlations. The urogenital papilla of female *Eleotris picta* is different from that of both *E. tubularis* and *E. tecta.* The posterior margin is not as rounded and has a fringe of finger-like projections that flare in the largest females (Fig. 3). Females of *E. tecta* and *E. tubularis* have robust, round urogenital papillae with fewer fringes. The urogenital papillae of female specimens of *Eleotris picta* develop more slowly then their smaller relatives. Among female specimens of *E. tecta* and *E. tubularis*, urogenital papillae vary little other than the development of longer pre-vent furrows in *E. tubularis* (Fig. 3). Urogenital papillae development in males occurs at a smaller size in *Eleotris tubularis* and *E. tecta* compared to *E. picta* (Fig. 4).

Principal components analysis of meristic features clearly separated the three species (Fig. 5). *Eleotris picta* has more predorsal scales than either eastern Pacific congener (Table 2). It also has more lateral scale rows than the others, but does overlap with *E. tecta. Eleotris tubularis* has a lower lateral scale count than either eastern Pacific congener (Table 2). When comparing transverse scale counts, *E. picta* has a much higher count than *E. tubularis*, whereas *E. tecta* has an intermediate range. *Eleotris tecta* is distinct from *E. picta* in having a lower range for caudal peduncle scale count, but is not distinguished by that feature from *E. tubularis* (Table 2). Although overlap occurs, the means and modes for pectoral-fin elements are distinct for each species. Modes observed were 18 for *Eleotris picta*, 17 for *E. tecta* and 16 for *E. tubularis* (Table 2). Principal components analysis of meristic characters among the regional samples of *Eleotris picta* suggested clinal variation from high values in the region of Guatemala-Costa Rica to lower values both southward and northward. The pattern reflected variation primarily of transverse scale row counts and caudal peduncle scale counts (Table 3). Specimens from Mexico (regions 1 and 2 in Table 3) also had higher numbers of lateral and predorsal scales.

Eleotris from the eastern Pacific differ consistently in cephalic free neuromast patterns (Fig. 2). Though intraspecific variation can be observed, species are distinguished by the number and specificity of transverse suborbital rows extending ventrally beyond horizontal row *d*, the presence of row *ot'*, and the union or separation of opercular rows *os* and *oi*. The transverse suborbital rows of *Eleotris picta* and *E. tubularis* have the same configuration, rows 2 and 4 extend well ventral to horizontal row *d* in both species (2.4 pattern), but additional segments, incompletely formed superficial rows occur between the transverse rows in *E. picta.* In contrast to its two congeners, transverse suborbital row 3 crosses horizontal row *d* in *E. tecta* (Fig. 2). The cephalic neuromast pattern of *E. picta* is also distinguished from those of *E. tecta* and *E. tubularis* by the addition of an opercular posterior vertical row *ot'*. In *Eleotris picta*, *ot'* connects with opercular row *os* to form a fork on the upper posterior portion of the opercle. Row *ot* continues obliquely to the margin of the opercle where it connects

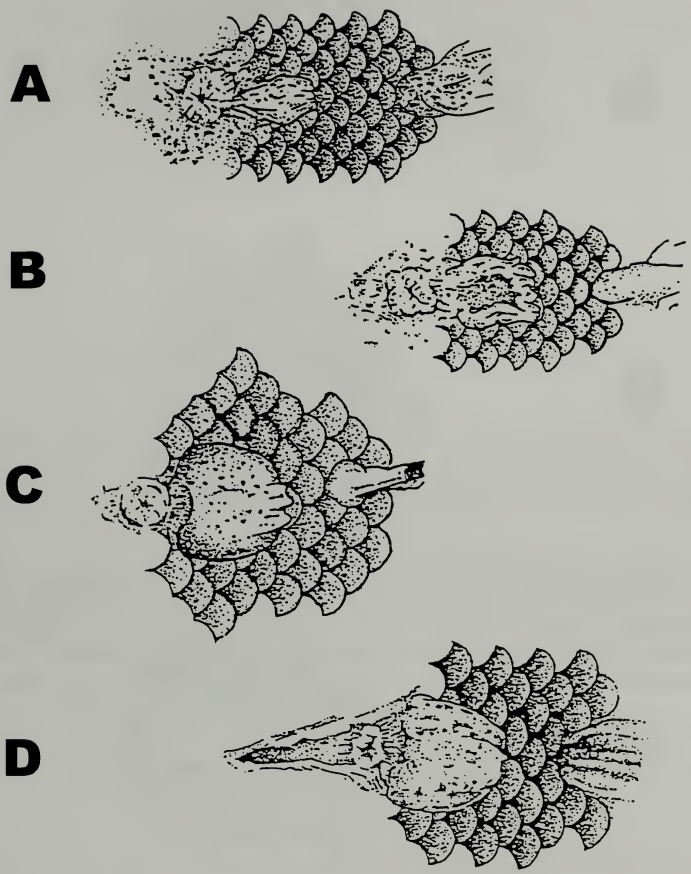

Figure 3. Comparison of the urogenital papillae among females of eastern Pacific *Eleotris*. a) *Eleotris picta* 63.7 mm SL (TNHC 14755) b) *Eleotris picta*, 63 mm SL (USNM 293478) c) *Eleotric tecta*, 55.1 mm SL (CAS 137539) d) *Eleotris tubularis*, 58.7 mm SL (LACM 200047).

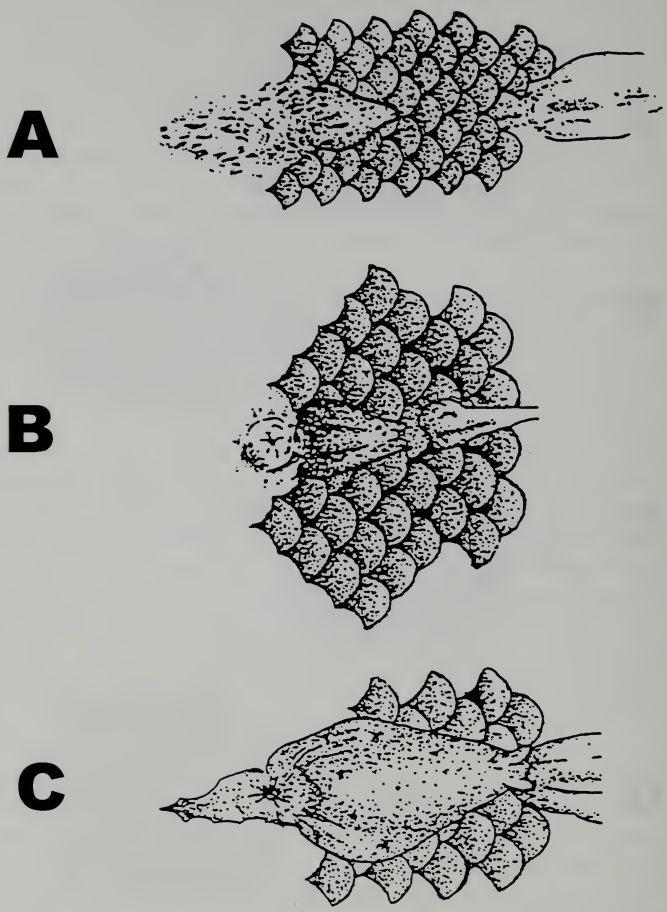

Figure 4. Comparison of urogenital papillae among males of eastern Pacific *Eleotris*. a) *Eleotris picta*, 51.4 mm SL (ANSP 144132) b) *Eleotris tecta*, 42.0 mm SL (CAS 66639) c) *Eleotris tubularis*, 50.5 mm SL (LACM 25806).

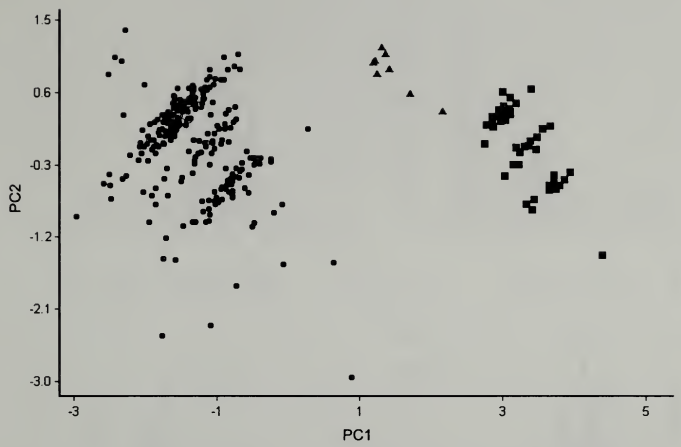

Figure 5. Principal components analysis of eastern Pacific *Eleotris* populations using meristic features (transverse scale rows, lateral scale rows, caudal peduncle scale rows, pectoral fin rays and predorsal scales). Dots = *Eleotris picta*, triangles = *E. tecta*, and squares = *E. tubularis*.

with lower longitudinal row *oi* (Fig. 2). *Eleotris tubularis* and *E. tecta* lack *ot'* altogether. The relationship between rows *os* and *oi* differs between *Eleotris tubularis* and *E. tecta*. The upper row *os* in *E. tecta* shifts obliquely downward to meet the posterior end of lower longitudinal row *oi* on the lower right posterior margin of the opercle. Intersection of upper row *os* and lower longitudinal row *oi* was not observed in specimens of *E. tubularis* (Fig. 2).

Although all three species have a basic brown body color, pigmentation varies among the species. *Eleotris tecta* has horizontal rows of spots along the sides and a prominent spot on the upper pectoral fin base. *Eleotris tubularis* lacks both well-defined rows of spots along the sides and the spot on the upper pectoral fin base. *Eleotris picta* has a dark band or row of blotches along the upper flanks, lacks the dark spot on the upper pectoral fin base and often has a mottled body.

Western Atlantic. The three western Atlantic species are not so easily delineated, but a combination of meristic, neuromast patterns and subtle pigmentation differences does allow their distinction. As with the eastern Pacific species, morphometry was of little help in distinguishing taxa, even with principal components analysis (Table 4).

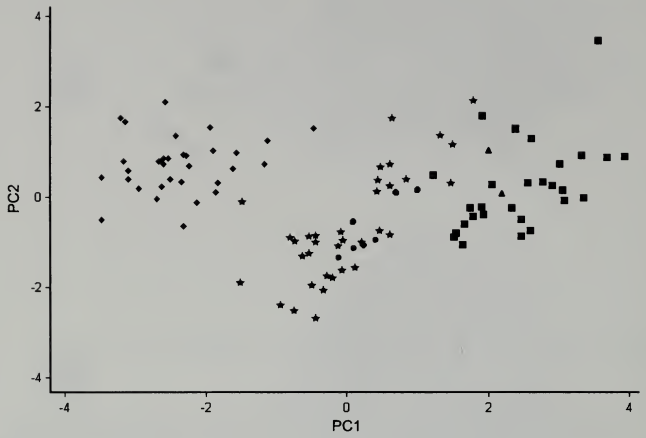

Figure 6. Principal components analysis of western Atlantic *Eleotris* populations using meristic features (transverse scale rows, lateral scale rows, caudal peduncle scale rows, pectoral fin rays and predorsal scales) and cephalic suborbital neuromast patterns. Diamonds = *Eleotris perniger*, stars = *E. pisonis*, dots = *E. amblyopsis* from the Gulf of Mexico, triangles = *E. amblyopsis* from SE Florida, and squares = *E. amblyopsis* from Central and South America.

Meristic and cephalic neuromast features clearly separate *Eleotris amblyopsis* and *E. perniger* (Fig. 6). The meristic differences are best illustrated by a comparison of lateral scale row counts (Table 5). *Eleotris amblyopsis* ranged from 40-58 with a mean of 49. *Eleotris perniger* had 54-68 with a mean of 60. The distinction between these two species is pronounced however, where they are sympatric in the Caribbean Basin; *E. amblyopsis* counts from that region ranged from 40-52 (Fig. 7 and 8). Lateral scale row number ranged from 47-63 with a mean of 54 for *Eleotris pisonis*. Although there was broad overlap with *E. amblyopsis*, *E. pisonis* counts were usually 50-54 in Guianas and eastern Venezuela where the two species are sympatric (Figs. 7 and 8). *Eleotris amblyopsis* counts ranged from 41- 46 in that region.

Cephalic free neuromast patterns distinguish *Eleotris perniger* from its two western Atlantic congeners (Fig. 9). Whereas *E. perniger* typically has a 2.4.6 transverse suborbital row pattern, the other two species have a 2.3.4 pattern.

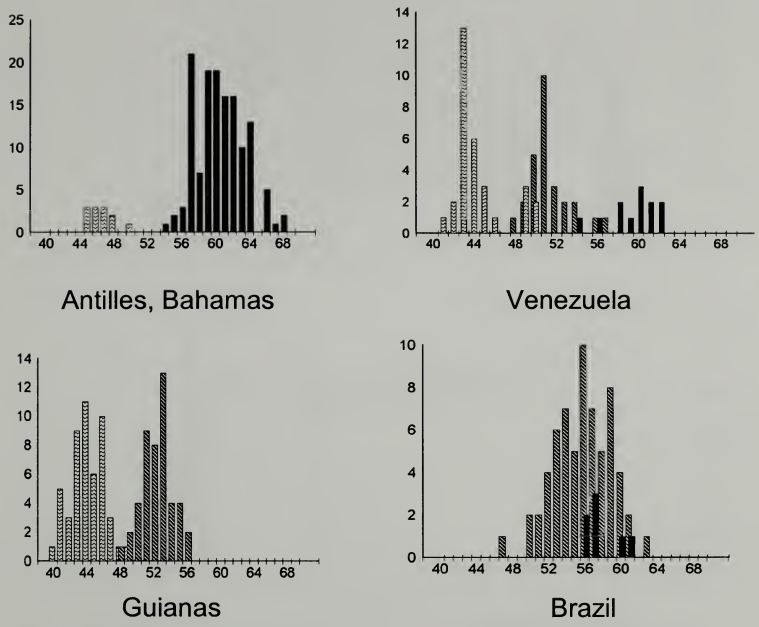

Figure 7. Frequency distributions of lateral scale counts (x axis) for western Atlantic *Eleotris* from South America, the insular Caribbean Basin and the Bahamas. Solid bars = *Eleotris perniger*, diagonal bars = *Eleotris pisonis* and wavy horizontal bars = *Eleotris amblyopsis*.

Eleotris perniger may also develop additional short segments between the primary rows. *Eleotris amblyopsis* from North America, particularly specimens seen from North Carolina, may have an additional row developed on one side of the head or the other. Many specimens from the Gulf of Mexico and the Carolinas also had occasional short segments developing between the primary rows. Intraspecific variation is detailed in the species accounts below. None of the western Atlantic species exhibit opercular row *ot*' and *os* and *oi* are generally connected although this may be variable within species.

Pigmentation is remarkably similar among the three western Atlantic species, and actually throughout the genus. Preserved specimens of all three species are basically tawny in body color with a light colored abdomen. *Eleotris perniger* tends to have well-developed horizontal rows of spots on the flanks that in some specimens appear as continuous lines. Of the other two species, *E.*

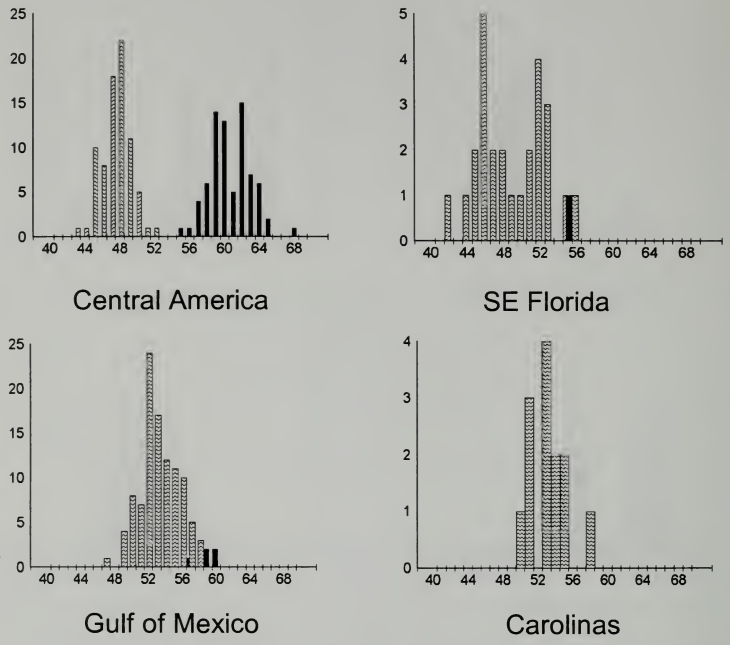

Figure 8. Frequency distributions of lateral scale counts (x axis) for western Atlantic *Eleotris* from North and Central America. Solid bars = *Eleotris perniger* and wavy horizontal bars = *Eleotris amblyopsis*.

amblyopsis may have horizontal rows of spots, but less regularly arranged or contrasted as in *E. perniger*. Most often, *E. amblyopsis* shows scattered spots along the upper flanks which may not be arranged in rows. *Eleotris pisonis* specimens were seen with the scattered spots as in *E. amblyopsis*, but sometimes spots on the sides were entirely lacking. *Eleotris perniger* and *E. amblyopsis* both have a dark spot on the upper pectoral-fin base. This spot was generally not observed in *E. pisonis*, but when it was expressed it was poorly contrasted and not as pronounced as dark pigment above the pectoral-fin base on the side of the nape. Individuals of any of these species or the eastern Pacific species may shift to a two-tone appearance of the trunk in which a light dorsum is sharply and evenly contrasted with dark flanks.

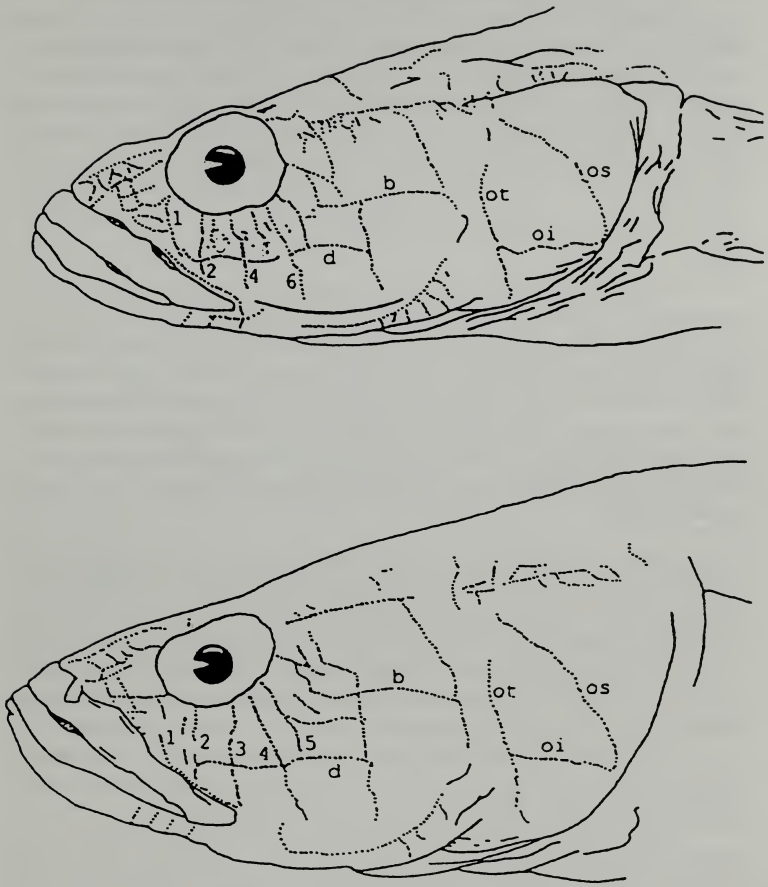

Fig. 9 Cephalic free neuromast patterns of western Atlantic *Eleotris* species, *E. perniger* (above) 57.5 mm SL, NLU 69725 and *E. amblyopsis* (below) 60.7 mm SL, NLU 69723. The suborbital free neuromast configuration of *Eleotris pisonis* (not illustrated) is the same as that shown for *E. amblyopsis*.

Discussion

Our findings support the recognition of six *Eleotris* species in the Western Hemisphere. Bussing (1996) and Miller (1998) have previously noted the conservative morphology of the genus. The only significant morphometric variation we observed was that of the form of the urogenital papilla, which is useful in determining the sex of individuals. Eye size was a major distinguishing feature in Jordan and Gilbert's (1896) original description of *E. abacurus* and a relatively larger eye size has been used since then to separate *E. amblyopsis* from *E. perniger* (referred to in most works as *E. pisonis*) in keys to eleotrids of the western Atlantic (e.g. Villa, 1982). We found no concordance between eye size variation and the other features determined diagnostic for the western Atlantic species.

Despite the importance of meristic characters in delimiting the species, some meristic features regarded as diagnostic in the literature were uninformative. Jordan and Evermann (1898) used the extent of cheek squamation to distinguish *E. amblyopsis* (including *E. abacurus*, a synonym herein) and *E. pisonis* from *E. perniger*. *Eleotris amblyopsis* and *E. pisonis* were described as having fully scaled cheeks, while those of *E. perniger* were only ½ scaled. We found cheek squamation highly variable within species. The extent of squamation on the snout and interorbital region, characters examined by Akihito (1967), were also of no utility.

Comparisons with West African species. *Eleotris daganensis* Steindachner, 1869 of the eastern Atlantic is indistinguishable from *E. amblyopsis* from the Caribbean Basin. The free neuromast patterns, number of lateral scale rows and body and fin pigmentation are similar in type and variation. The number of scales in a lateral series ranged from 44 - 53 with a mean of 48 in 48 specimens of *E. daganensis* examined. Specimens of that species typically had a 2.3.4 suborbital neuromast pattern, but of 38 examined one had a 2.3.5 pattern and another 2.3.4.5. Undoubtedly, *E. amblyopsis* and *E. daganensis* are closely related and possibly sister species. Their relationship to *E. annobonensis*, *E. perniger* and *E. pisonis* is close and undecipherable from comparative morphology.

Eleotris annobonensis from the eastern Atlantic islands of Equatorial Guinea and Pagalu (Annobon) is similar to *E. perniger*. Pigmentation is comparable between these two species and lateral scale row numbers are the same. Suborbital free neuromast patterns differ slightly in the extent of supernumerary row development. Whereas 2.4.6 is the predominant pattern in *E. perniger*, 2.3.4 with intervening segments was the most common pattern observed in the 22 specimens of *E. annobonensis* we examined, including types. Only 3 specimens had a 2.4.6 pattern; one specimen had a 2.4 pattern and another a 2.5.8 pattern.

Of all the *Eleotris* species in the eastern Pacific and Atlantic basins, *Eleotris picta* is most similar to *E. senegalensis*, *E. feai* and *E. vittata* from West Africa. All four species have the forked neuromast pattern on the upper operculum. All are large species for the genus, with *E. picta* possibly reaching the largest size. *Eleotris picta* is similar in lateral scale row number to *E. vittata* and *E. feai*. Twenty specimens of *E. vittata* had a range of 57-65 and a mean of 61. Two paratypes of *E. feai* had counts of 62 scales. Although *E. senegalensis* has larger scales (and therefore a lower count), most specimens examined exhibited a 2.4 suborbital neuromast row pattern as in *E. picta*. There was variation observed for this feature in both *E. vittata* and *E. senegalensis*, however. The 19 specimens of *E. vittata* examined for the character showed five patterns - 2 (15 specimens), 3 (1), 2.3 (1), 2/2.5 (1) and 2.4/2.5 (1). The *E. feai* paratypes had 2 and 2/2.5 patterns. Twenty-one specimens of *E. senegalensis* showed 2 character states - 2 (3) and 2.4 (18). A low degree of variation for this feature was also observed in *E. picta*; out of 255 specimens examined, four had 2.3.4 and one a 2.3.4.5 pattern. Of the four with the 2.3.4 pattern, only one had the aberrant pattern on both cheeks. Clearly, the phylogenetic lines of *Eleotris* hypothesized by Miller (1998) based upon differences in suborbital neuromast patterns may be confused when variation is considered. The potential for homoplasy is great.

Eleotris amblyopsis is not synonymized with *E. daganensis* and *E. perniger* is not synonymized with *E. annobonensis*. The allopatric distributions of these taxa make it difficult to evaluate the relationships of the amphi-Atlantic species pairs considering the scant, subtle and overlapping morphological variation of diagnostic characters observed among the western Atlantic taxa. For example, although North American populations of *E. amblyopsis* approach a morphology that could be confused with that observed in *E. perniger*, sympatric populations of the two species in the Caribbean Basin are clearly distinguished. Additionally, the distinctive compositions of the west African and western Atlantic gobioid faunas suggest that gene flow between gobioid fishes of these two long-isolated regions is unlikely, even considering the pelagic larval stage of these species. It is most parsimonious and consistent with the Evolutionary Species Concept not to synonymize the species pairs. There is considerable circumstantial evidence to suspect that these taxa have had independent evolutionary histories for millions of years and continue on distinct evolutionary trajectories. We also believe that application of the Morphological Species Concept to this genus of cryptic species is inappropriate because of the concept's insensitivity to the diversity the genus comprises.

The gobioid fauna of tropical West Africa comprises about 28 genera, including 8 that are endemic to that region and two others endemic to Africa (Birdsong et al., 1988). Three genera are shared with the Indo-Pacific (discounting the introduced *Prionobutis*) and four genera are shared only with the northeastern Atlantic/Mediterranean region (Table 6). Five genera are shared only with

the Western Hemisphere. Five other genera are more cosmopolitan, occurring in the Western Hemisphere, Indo-Pacific and eastern Atlantic. Thus, of the 28 gobioid genera in West Africa, 10 are shared with the Western Hemisphere. One goby species possibly common to the eastern and western Atlantic, *Bathygobius soporator* (Miller and Smith, 1989), doesn't increase the likelihood of ongoing gene flow among other gobioids. It merely suggests a lack of differentiation despite a long period of isolation and offers no evidence of even an intermittent mechanism for larval transport east to west across the Atlantic. It should also be noted that there are five species of *Eleotris* in the eastern Atlantic, three of which (*E. feai*, *E. senegalensis* and *E. vittata*) have no counterpart in the western Atlantic. It seems unlikely that there should be any link between populations of *E. daganensis* or *E. annobonensis* and their New World counterparts, and not the other three species if east to west surface currents are the potential vehicle.

Miller (1998) suggests that a subsurface equatorial countercurrent could allow dispersal from west to east across the Atlantic. Studies of larval gobiids have shown a typical duration of 20 - 40 days (Breitburg, 1989; Brothers et al., 1983; McFarland et al., 1985). This is a much shorter period than the 96 days estimated as necessary for cross Atlantic subsurface transport at the equator (Scheltema and Hall, 1975). The western Atlantic has more than 120 gobioid species (Birdsong et al., 1988) and an entire tribe, the Gobiosomini, that is shared only with the more recently conjoined eastern Pacific. This degree of taxonomic distinction is consistent with the limitations on larval transport that may be inferred from the few studies mentioned above. However, a much longer larval period was observed by Radtke et al. (1988) for the Hawaiian freshwater gobiids *Stenogobius genivittatus* and *Awaous stamineus* that would span the 96 days estimated above. Studies of shore fishes of the St. Paul's Rocks (Lubbock and Edwards, 1981), St. Helena (Edwards and Glass, 1987) and Ascension Islands (Lubbock, 1980) are informative. No gobioid fishes were taken at St. Pauls' Rocks. Two gobies are known from Ascension and St. Helena, the western Atlantic *Gnatholepis thompsoni* and the endemic *Priolepis ascensionis*. One specimen of an *Eleotris* species was captured at St. Helena and referred to *E. pisonis*. This species' identity has not been checked by us. These mid-Atlantic tropical islands are more interesting for the gobioid species they lack, than for those that are present. The lack of more of the rocky reef-associated goby fauna suggests a passage too long or stressful for most gobioid fishes. Where is *Bathygobius soporator*? As for the single sleeper at St. Helena, was it a ballast introduction as we presume for the *Eleotris picta* specimen we have observed from Venezuela?

There is limited information available about the status of tropical Atlantic species within the ten gobioid genera common to both sides of the ocean, but it generally suggests isolation of the shore fauna. The only other shared eleotrid genus is *Dormitator*, the common west African species, *D. lebretonis*, is distinct

from the common western Atlantic species, *D. maculatus* (unpubl. data). The species limits and relationships within *Sicydium*, the only sicydiine genus common to streams in both the Caribbean Basin and Gulf of Guinea, are unclear, but Harrison (1993) observed that *S. bustamantei* from West Africa and specimens identified as *S. plumieri* from the Antilles were very similar and suggested that they could be amphi-Atlantic conspecifics as has been suggested for *Bathygobius soporator*. Watson (2000) redescribed *S. plumieri*, but did not include *S. bustamantei* in the synonymy. Although he indicated some familiarity with West African species, he did not list any comparative material from West Africa, so the question of species distinction remains unanswered. Among the shared gobionelline genera, *Awaous*, *Ctenogobius*, *Gnatholepis*, *Gobioides* and *Gobionellus*, information on species status is available for three genera. In a recent review of the genus *Gobioides*, Murdy (1998) recognized two African species distinguished from western Atlantic species. *Gobionellus* and *Ctenogobius* are each represented by a single species in West Africa not found in the western Atlantic (Pezold, 1984). Reports of *Gobionellus oceanicus* from (e.g. Miller and Harrison, 1992) the Gulf of Guinea are presumed to be based on misidentifications of *G. occidentalis* as no specimens of this species were found from West Africa during an exhaustive review of the genus (Pezold, 1984). The gobiine genus *Priolepis* has not been reviewed for its Atlantic species.

The phylogenetic relationships of species within the 10 shared genera are for the most part unknown. Murdy (1998) offers evidence that *Gobioides africanus* is the sister group to the other species of the genus. Preliminary data also indicate that *Dormitator lebretonis* is the primitive sister group to the Western Hemisphere species (unpubl. data). These observations further support a long break between gobioid populations on the two sides of the Atlantic.

Instead of any active genetic exchange across the Atlantic we suggest that *Eleotris* is simply morphologically conservative. Similar morphotypes to those seen in the Western Hemisphere and the eastern Atlantic pop up in other tropical estuaries and insular streams, albeit ever so slightly different. Present circumglobal distributions suggest that several basic lines were separated long ago. This perspective is reinforced by the phylogenetic study of gobioid fishes using mtDNA by Akihito et al. (2000). The several species of *Eleotris* included in their analysis, *E. acanthopoma*, *E. fusca*, *E. melanosoma* and *E. oxycephala* were separated by greater genetic distances than were specimens in the morphologically distinct pairs of genera *Dormitator* and *Hypseleotris*, and *Calumia* and *Gobiomorphus*. The four species of *Eleotris* are distinguishable by cephalic free neuromast patterns and various meristic combinations similar to those seen in the Western Hemisphere.

Phylogenetic Relationships. Miller (1998) subdivided *Eleotris* into clusters of nominal species based upon cephalic neuromast patterns. Although there is

heuristic value in his approach, cephalic free neuromast patterns must be used with caution in any phylogenetic reconstruction. The suborbital row patterns vary additively and ontogenetically, and that variation is significant, as can be seen in the species descriptions that follow. Variation among species also exists for the presence or absence of the *ot'* row that Miller regarded as a synapomorphy for *Leptophilypnus* and *Eleotris* (including *Erotelis*). In addition to the variation among *Eleotris* species as noted by Miller, it appears in only one of the two *Leptophilypnus* species; *Leptophilypnus fluviatilis* has it, but *L. panamensis* does not. The appearance of both states of the single proposed synapomorphy in *Leptophilypnus* increases the homoplasy inherent in any phylogenetic reconstruction and weakens the argument for recognizing *Leptophilypnus* as the sister group to an *Eleotris* clade on the basis of that character alone. Before an unequivocal phylogeny of intrageneric relationships can be developed, more polarized characters are needed, and this demands a better understanding of eleotrid relationships. Another major problem confronting any attempt at phylogenetic reconstructions of intrageneric *Eleotris* relationships at this time is that morphological variation within and among Indo-Pacific species requires attention. The seminal work by Akihito (1967) was only a beginning.

Systematics

Eleotris Bloch and Schneider, 1801

Eleotris, Bloch and Schneider (1801): 65. Type species: *Gobius pisonis* Gmelin 1789, South America (Brazil). Type established by ICZN by use of plenary powers (Opinion 93, Direction 56) and *Eleotris* Gronow 1763 listed as a name published in a rejected work (Opinion 417).

Eleotrides, Bory de Saint-Vincent, 1825: 417. Type species: *Gobius pisonis* Gmelin 1789.

Culius, Bleeker, 1856: 385, 411. Type species: *Cheilodipterus culius* Hamilton 1822, Bengal, India, by absolute tautonymy, not *Culius fuscus* Bleeker 1856 (= *Poecilia fusca* Bloch and Schneider, 1801 = *Eleotris nigra* Quoy and Gaimard, 1824, 259, pl 60 fig 2, Waigeo, Indonesia) as subsequently designated in Bleeker 1874: 303.

Kieneria, Maugé, 1984: 98 (subgenus of *Eleotris*). Type species: *Kieneria vomerodentata* Maugé, 1984, Madagascar, by original designation and monotypy.

Diagnosis. Eleotrid fishes with transverse suborbital free neuromast rows, no cephalic lateralis canals, a spine on the angle of the preopercle, and equal numbers of fin elements in the second dorsal and anal fins (I,8).

DESCRIPTION. Head broad and flattened, body low, and torpedo-like. Mouth large and oblique, posterior margin of upper jaw to vertical through middle of eye or rear margin of orbit, lower jaw projecting. Upper and lower jaws with multiple rows of small teeth, a few caniniform teeth in some species. Tubular anterior nares overhanging upper lip, posterior nares open pits. Stout antrorse spine at angle of preopercle. Small eyes high on head. Interorbital broad, frequently three times eye width. Gill opening moderately broad, extending to below preoperculum. Almost completely scaled, cycloid scales on nape, cheek, opercle, interorbital, pectoral-fin base, pre-pelvic region, abdomen, and in one or two rows bordering median fins, ctenoid scales covering sides of trunk. Urogenital papilla in females rounded, bulb-shaped with orifice equal to anus in size, elongate and tapered in males. Pectoral fins longer than pelvic fins, variably reaching to vertical through urogenital base to vertical through anal-fin origin. Pelvic fins separate, I, 5, generally not reaching anus (variable within *E. amblyopsis*, may reach anus in some populations). Two separate dorsal fins, first dorsal fin with six flexible spines, second dorsal fin with single leading flexible spine followed by eight soft rays. Anal fin with single flexible spine followed by eight soft rays. Appressed median fins not reaching caudal-fin base. Caudal fin rounded, preceeded by 8-10 procurrent fin rays that extend forward no further than above the penultimate caudal vertebra. Caudal fin not extended forward along the caudal peduncle. No lateral line canals. Rows of transverse and longitudinal free neuromasts (sensory papillae) on head; disconnected short vertical rows of free neuromasts along sides of trunk; three diverging rows of free neuromasts on caudal fin, central row horizontal, upper and lower rows angled posterodorsally and posteroventrally respectively. Dorsal-fin pterygiophore formula 3-1221 or 3-12210, 10 + 15 = 25 vertebrae, two epurals, 2 or 3 preanal hemal pterygiophores (Birdsong et al., 1988).

REMARKS. *Eleotris* was placed in the Official List of Generic Names and *Gobius pisonis* Gmelin,1789 was established as the type species by the International Commission on Zoological Nomenclature by use of plenary powers for the suspension of rules in Opinion 93, Direction 56, 1926. The summary lists *E. gyrinus* Cuvier and Valenciennes as type species in error. Opinion 93 also notes that *Gobiomoroides*, Lacepède, 1800: 592, is not a synonym of *Eleotris* as the dried type specimen has a "single dorsal of 45 rays and canine teeth." *Epiphthalmus*, Rafinesque- Schmaltz, 1815: 86, an unnecessary substitute name for *Gobiomoroides,* is also removed from synonymy.

Miller (1998) synonymized *Erotelis* with *Eleotris* because they share an antrorse spine on the preoperculum, have the same number of precaudal and caudal vertebrae, agree in first dorsal-fin pterygiophore pattern and have similar cephalic sensory systems. He stated that they only differ in squamation. *Erotelis* has small cycloid scales covering the body, while *Eleotris* has larger scales and those on the lateral trunk are ctenoid. In actuality, *Erotelis* also differs in having a

derived condition of the caudal fin. The caudal fin is tapered and has 12-14 unsegmented procurrent rays before the hypural both dorsally and ventrally that extend forward above and below the third caudal vertebra from the terminus. The procurrent rays are elongate and support well-developed fin margins along the rear portion of the caudal peduncle. In *Eleotris*, there are about eight to ten rays in advance of the hypural extending no farther forward than above and below the penultimate caudal vertebra and the caudal fin is rounded. The procurrent rays of *Eleotris* also quickly taper to rudiments and are not associated with extensive fin membranes as seen in *Erotelis*. *Erotelis* also has a much more oblique jaw, a more elongate body, more segmented rays in the second dorsal and anal fins, one more ray in the second dorsal fin than the anal fin (as opposed to equal numbers) and a highlighted myomeric pattern of pigmentation on the sides (Dawson, 1969; Ginsburg, 1953; Jordan and Evermann, 1898). We assume that Miller's purpose in synonymizing the two genera was to establish a monophyletic *Eleotris* based upon the shared possession of a preopercular spine. As none of the other characters of the axial skeleton and cephalic lateralis are unique to *Eleotris*, the genus remains undefined by a synapomorphy. The number of elements in the second dorsal fin and anal fin, as a combination, may be synapomorphic, but this character cannot be polarized until an outgroup is unequivocally identified. Accepting the preopercular spine as a synapomorphy of the two genera, the three *Erotelis* taxa (two species and a subspecies) are characterized by several derived features: many small cycloid scales covering the body, the lanceolate caudal fin, the forward extensions of the caudal fin and their numerous associated procurrent rays and probably the myomeric pigmentation on the sides. Polarity of the other characters described for *Erotelis* is less certain. Considering the conservative nature of morphological variation within *Eleotris* and other genera of eleotrids, the distinction of *Erotelis* from *Eleotris* is outstanding. Synonymization will only obscure the distinctions. If we were to apply the same rationale to gobioid fishes as a whole, that is ignoring identified monophyletic groups if it results in a sister group diagnosed by plesiomorphic traits, we would only have two families, Rhyacichthyidae and Gobiidae with all but a couple of the roughly 2000 gobioids in the latter family (Miller, 1973). Obviously much information is less readily available in a classification developed with that approach and many of our advances in understanding of gobioid relationships would be less apparent (e.g. Hoese and Gill, 1993; Pezold, 1993). We recognize the two genera as distinct and valid.

Key to *Eleotris* species of the Western Hemisphere

1. a. Teeth heteromorphic, several rows of fine teeth in both jaws with larger canine teeth present laterally towards rear in outer row

and/or medially near symphysis in inner rows; opercular free neuromast row *ot'* absent.....2
b. All teeth fine, no canine teeth present; opercular vertical row *ot'* present.....*E. picta*
(eastern Pacific; Mexico to Peru and the Galapagos)

2. a. Dark spot present on upper pectoral-fin base (may be covered by opercular membrane), darker than markings on nape at opercular margin.....3
b. No dark spot present on upper pectoral-fin base or if present not strongly-contrasted and not as dark as pigment on nape.....4

3. a. Second and some combination of two of third, fourth or fifth transverse suborbital neuromast rows extend below longitudinal row *d* (usually third and fourth).....5
b. Second, fourth and sixth transverse suborbital neuromast rows extend below longitudinal row *d*.....*E. perniger*
(western Atlantic; Caribbean Basin, Mexico, Bermuda)

4. a. Only second and fourth transverse suborbital neuromast rows on cheek extend below longitudinal row *d* (2.4 pattern)...*E. tubularis*
(eastern Pacific; Cocos Island)
b. Second, third and fourth transverse suborbital neuromast rows on cheek extend below longitudinal row *d* (2.3.4 pattern)...*E. pisonis*
(western Atlantic; Brazil to Orinoco delta)

5. a. Scales in lateral series 40-58 over range, 43-52 in Caribbean Basin.....*E. amblyopsis*
(western Atlantic; primarily continental, Guianas through North Carolina, Cuba, occasional other Antilles)
b. Scales in lateral series 54-60.....*E. tecta*
(eastern Pacific; Costa Rica through Colombia)

Eleotris amblyopsis (Cope, 1871)

Eleotris gyrinus, Valenciennes, in Cuvier and Valenciennes, 1837: 220, pl. 356, Martinique and Saint-Domingue, (in part).
Culius amblyopsis Cope, 1871: 473, Surinam.
Eleotris (Culius) belizianus Sauvage, 1880: 56, Belize, (in part).
Eleotris abacurus Jordan and Gilbert, 1896: 228, Charleston, South Carolina.
Eleotris isthmensis Meek and Hildebrand, 1916: 356, 359, Mindi, Panama Canal Zone.

DIAGNOSIS. Scales in lateral series 40 - 58, generally 41- 46 in NE South America, 45 - 49 in Caribbean Basin, 50 - 56 in North America. Second, third and fourth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* (2.3.4 pattern); lacking *ot'* neuromast row on upper opercle. Dark blotch present on upper pectoral-fin base; sides of trunk usually with scattered spots along dorsum and no regular rows of spots of uniform intensity forming horizontal pinstripes.

DESCRIPTION. Body morphology as described for genus. Both jaws with multiple rows of fine teeth, larger canine teeth present laterally towards rear in outer row and/or medially near symphysis in inner rows. Proportional measurements are given in Table 4.

Meristics. First dorsal fin VI; second dorsal fin I,8 (I,7-I,9); pectoral fins 16 (15-18); pelvic fins I, 5; anal fin I,8 (I,7-I,8). Scales in lateral series 49 (40-58), generally 43-46 in NE South America, 45-49 in Caribbean Basin, 50-56 in North America; predorsal scales 36 (29 - 46); transverse scale rows 14 (11 - 18); caudal peduncle scale rows 15 (11 - 24).

Cephalic lateralis. Fig. 9. Five transverse suborbital free neuromast rows of which 2nd, 3rd and 4th extend ventrally beyond horizontal row *d* (2.3.4 pattern). Short supernumerary segments may occur between two or more transverse rows in specimens from North America, occasionally with an extra row on one or both sides such that 2nd, 3rd and 5th (2.3.5) or 2nd 4th and 5th rows (2.4.5) extend below row *d*, extra rows especially common in specimens from Atlantic coast of US. No *ot'* row on upper opercle, row *os* connects with row *oi* at ventroposterior margin of opercle.

Coloration in alcohol. Based on specimens from Costa Rica (NLU 69723), Florida (UF 87886), and Mexico (UMMZ 209724). Body dark brown laterally, lighter along the dorsum or tan with rows of spots on sides of varying intensity; abdomen and gular region lighter. Cheek with two dark streaks radiating posteriorly from eye, one along sulcus between nape and cheek and operculum. Large spot on upper pectoral-fin base which may be covered by the opercular membrane; two elongate spots extending from pectoral-fin base onto pectoral-fin rays seen in some specimens. First dorsal fin with dark band along base and another reticulate band through middle of fin, dark spots generally present on spines above mid-level band, but not at tips, bands generally converging posteriorly; second dorsal fin with 5 to 8 wavy diagonal bands, sometimes over dusky membrane; anal fin dusky or with as many as seven wavy rows of spots; caudal fin with 10 to 14 vertical bars formed by small spots on rays against a dusky mem-

brane; pectoral fins peppered with small spots on rays, membrane may be clear or dusky, pelvic fins similar but with fewer rows of spots.

DISTRIBUTION. Common in continental estuaries from French Guiana to North Carolina, but also known from Brazil and the Antilles. Enters freshwater streams in the Caribbean Basin.

COMMENTS. This species reaches a smaller maximum size than *E. perniger* and matures at a size of 50-60 mm (Hildebrand, 1938). The largest specimen collected by Greenfield and Thomerson (1997) in Belize was just over 73 mm SL and Bussing (1996) reported it to reach 80 mm SL in Costa Rica. The largest specimens observed in our study were 83 mm SL from the Caribbean Basin and 113 mm SL from North America.

Dawson (1969) noted the ability of this species to change color pattern from uniformly dark to dark laterally with a light dorsum, a trait that seems to be common to a number of *Eleotris* species. This is most likely the species from Mexico karyotyped by Uribe et al. (1994), as *E. perniger*, though known from that region, is not the common species. Karyotypes revealed heteromorphic sex chromosomes; 44 acrocentric and two metacentric chromosomes.

This species is known from both estuaries and streams in Central America (Gilbert and Kelso, 1971; Greenfield and Thomerson, 1997; Nordlie, 1979) where it often co-occurs with *E. perniger* and estuaries in North America (Dawson, 1969; Schwartz, 1999). In Belize, it was the primary species on the mainland (only one specimen of *E. perniger* was taken), but both species were regularly found together in Saint George's Cay on the barrier reef (Greenfield and Thomerson, 1997). Greenfield collected both species in Honduras, where *E. amblyopsis* was most common in estuaries and *E. perniger* (reported as *E. pisonis*) was found more often in freshwater. Gilbert and Kelso (1971) and Bussing (1998) found *E. amblyopsis* the more common species in Costa Rica. Although Gilbert and Kelso (1971) took both species together from estuaries and streams, Nordlie (1979) reported *E. perniger* (as *E. pisonis*) more common in freshwater than *E. amblyopsis*, but *E. amblyopsis* the more abundant by far in the Tortuguero estuary. Bussing (1998) also noted it in estuaries and streams to 15m elevation. In Panama *E. amblyopsis* was reported by Hildebrand (1938) (as *E. isthmensis*) to be less common than *E. perniger* (identified as *E. pisonis*). Although usually noted from low salinity estuaries in North America (e.g. Dawson, 1969), Gilmore and Herrema (1981) found them most common in freshwater in east-central Florida. Microhabitat preferences that have been noted included mangroves in Mexico (Britton and Morton, 1989), mangrove channels in Belize (Greenfield and Thomerson, 1997) and hyacinth roots in Costa Rica (Gilbert and Kelso, 1971). In Louisiana, the first author has collected this species associated with hyacinth roots and *Phragmites* marshes in oligohaline estuaries at

the mouth of the Mississippi River. Others have been captured in a channel in a *Spartina* marsh using traps composed of oyster shells in plastic crates. *Eleotris amblyopsis* is a carnivorous species that feeds on arthropods and fishes (Bussing, 1998; Nordlie, 1981). Nordlie observed no change in diet associated with position in the estuary or size.

Eleotris perniger (Cope, 1871)

Eleotris gyrinus, Valenciennes, in Cuvier and Valenciennes, 1837: 220, pl. 356, Martinique and Saint-Domingue, (in part).
Culius perniger Cope, 1871: 473, St. Martin, West Indies.
Eleotris maltzani Hilgendorf, 1889: 53, Haiti.
Eleotris hilgendorfi Pietschman, 1913: 182. replacement name for *E. maltzani* Hilgendorf (not Steindachner)

DIAGNOSIS. Scales in lateral series 54-68, usually about 60. Second, fourth and sixth suborbital free neuromast rows on cheek extending ventrally past horizontal row *d* (2.4.6 pattern), with numerous short segments above row *d* between transverse rows, sometimes an additional row formed resulting in 2.4.7 pattern or other variants; lacking *ot'* neuromast row on upper opercle. Dark blotch present on upper pectoral-fin base, sides of trunk usually with regular rows of spots or stripes.

DESCRIPTION. Body morphology as described for genus. Both jaws with multiple rows of fine teeth, larger canine teeth present laterally towards rear in outer row and/or medially near symphysis in inner rows. Proportional measurements are given in Table 4.

Meristics. First dorsal fin VI; second dorsal fin I,8 (I,7-I,8); pectoral fins 18 (16-19); pelvic fins I, 5; anal fin I, 8. Scales in lateral series 60 (54-68); predorsal scales 49 (39 - 62); transverse scale rows 20 (17-23); caudal peduncle scale rows 17 (13 - 21).

Cephalic lateralis. Fig. 9. Adults with six transverse suborbital free neuromast rows of which 2nd, 4th, and 6th extend ventrally beyond horizontal row *d* and many short supernumerary segments often present between transverse rows (2.4.6 pattern). Often one or two complete extra rows formed on one or both sides such that 2nd, 4th and 7th rows extend below row *d* (2.4.7), occasionally other patterns produced including 2.5.7, 2.5.8, 2.4.5, 2.4.8, 2.5.9, 2.6.8, 3.5.7 and 3.5.10. No *ot'* row on upper opercle, row *os* connects with row *oi* at ventroposterior margin of opercle. Early juveniles with five transverse suborbital rows forming 2.3.4 pattern and no intervening segments.

Coloration in alcohol. Based on specimens from Costa Rica (NLU 60725), Honduras (UF 16325, UF 16333), Mexico (UMMZ 196529), Panama (ANSP 104096, ANSP 104158, ANSP 104400), Puerto Rico (ANSP 115625, ANSP 144626). Body dark brown laterally, lighter along the dorsum or tan with rows of dark brown spots on sides sometimes forming thin horizontal pinstripes; abdomen and gular region lighter. Cheek with two dark streaks radiating posteriorly from eye, one along sulcus between nape and cheek and operculum. Large spot on upper pectoral-fin base which may be covered by the opercular membrane. Other pigment as observed in *E. amblyopsis*.

DISTRIBUTION. Common in the Caribbean Basin, predominant species in the Antilles, also known from Bermuda and Rio de Janeiro.

COMMENTS. Recent references to *Eleotris pisonis* from the Caribbean Basin (e.g. Bussing, 1998; Greenfield and Thomerson, 1997) in which large-scaled species (*E. amblyopsis*) and small-scaled species (*E. pisonis*) were distinguished refer to this species. This is the largest species native to the western Atlantic. Bussing reported that *E. perniger* reaches 120 mm SL. The largest specimen observed in our study was 177 mm SL. Doug Smith (pers. comm.), University of Massachusetts at Amherst, photographed a specimen captured on St. John Island, VI, that was approximately 250 mm TL. Considering that the caudal fin in this species averages 26% SL, the specimen was about 200 mm SL.

Greenfield and Thomerson (1997) reported a single juvenile specimen from freshwater in continental Belize where *E. amblyopsis* is the more abundant species. Hildebrand (1938) reported *E. perniger* as the common species in Panama. It is the only species known from Bermuda where Smith-Vaniz et al. (1999) reported two specimens from oligohaline waters: Walsingham Cave Pool and Fern Sink Cave Pool. Bohlke and Chaplin (1993) noted two juveniles from a shallow tidal creek on the south shore of New Providence Island. The specimens were collected over a substrate of sand and rocks amid mangrove roots. They stated that it was also known from freshwater Lake Killarney on that island. Bussing (1998) regarded *E. perniger* as uncommon in Costa Rica. He also said that it occurred in stagnant waters, or low velocity rivers and creeks. He found the species in water of 25-28 C and although most abundant near the coast, it occurs at least 60 m above sea level (which puts it farther inland than *Eleotris amblyopsis*). Like *E. amblyopsis*, it feeds primarily on fishes and shrimps. Nordlie (1979) found them mostly in freshwaters of the Rio Tortuguero system.

Eleotris picta Kner, 1863

Eleotris picta Kner, 1863:223. Rio Bayano, Panama.
Eleotris pictus Kner and Steindachner, 1864:18, Plate 3, fig. 1,

Rio Bayano, Panama. (spelled *Eleotris picta* on plate).
Culius aequidens Jordan and Gilbert, 1882:461, Rio Presidio near Mazatlan, Mexico.

DIAGNOSIS. Scales in lateral series 56-68, mode of 61. Neuromast configuration with second and fourth suborbital vertical rows extending ventrally past horizontal row *d* (2.4 pattern); opercular vertical rows *os* and *ot'* intersect on posterior opercle forming an acute fork opening towards posterior margin. Urogenital papillae small and square in shape in young females; distal margin fringed and flared in adult females; pre-vent furrow not well developed.

DESCRIPTION. Body morphology is as described for the genus, although the head is flatter and narrower compared to *Eleotris tubularis*. Broad bands of fine teeth in both jaws, no canine teeth. Urogenital papillae small and square in shape in young females; distal margin fringed and flared in adult females; pre-vent furrow not well developed. Proportional measurements are shown in Table 1.

Meristics. First dorsal fin VI; second dorsal fin I,8; pectoral fin 18 (11-19); pelvic fins I, 5; anal fins I,8 (I,8-I,9). Scales in lateral series 61 (56-68); predorsal scales 61 (53-65); transverse scale rows 24 (20-31); caudal peduncle scale rows 18 (13-23).

Cephalic lateralis. Fig. 2. Five suborbital transverse rows of which the 2nd and the 4th extend below horizontal row *d* (2.4 pattern). Supernumerary segments occur between the 5 transverse rows. Opercular vertical row *ot'* is present, connecting with horizontal row *os* to form an acute fork opening toward the posterior margin of the opercle.

Coloration in Alcohol. Based on specimens from Honduras (TU 186087) and Costa Rica (TU 84544, TU 24181, TU 84587, TU 84687 and TU uncat.). Color dark tan or brown with darkest pigment laterally on trunk. Abdomen pale. Entire body often mottled. Two dark postocular stripes present, more distinct in young; uppermost postocular stripe extends horizontally from orbit to posterior opercular margin; lower postocular stripe extends to upper preopercular margin. Pigmentation on lateral scales may form dark band, especially in juveniles, continuous or broken into series of large blotches, band being formed from horizontal rows of spots; often with dark speckles on top of head highlighting longitudinal rows of free neuromasts. All fins possess wavy, dusky bands of spots. Dorsal and ventral spots sometimes present above and below hypural.

DISTRIBUTION. Common from Mexico to continental Ecuador and the Galapagos

Islands, also known from Cocos Island and Salton Valley of California.

COMMENTS. This is the largest species of *Eleotris* in the Western Hemisphere. Bussing (1998) stated that it reaches 320 mm SL. The largest specimen we examined was 276 mm SL. Uribe and Diaz (1996) described the karyotype for this species as 52 acrocentric chromosomes.

Bussing (1998) described life colors of *Eleotris picta* as grayish black dorsally, with pale gray sides occasionally marked with irregular yellow blotches, and a tan abdomen with yellow or white blotches on young and subadults. He also stated that juveniles are often pale yellowish brown above with spotted sides and have a black tail with transparent margin. The fins in this species were noted as dark with transparent spots producing bands, although he notes that this pattern is less apparent in larger specimens. Grove and Lavenberg (1997) described the species as being dark greenish brown with a light abdomen with dusky fins "with dark speckles, [and] undulating stripes on the dorsal and anal fins". Juveniles were described as "mottled with blue and dark brown speckles, without stripes or bars."

Grove and Lavenberg (1997) reported one specimen 94 mm SL from a freshwater stream near Playa Negra, on Floreana in the Galapagos Islands. Bussing (1998) found them in waters ranging from stagnant to high velocity rivers. He reported them most abundant near the coast, but inhabiting streams up to 100 m above sea level, with larger individuals upstream. Temperatures at capture were from 25-33 C.

According to Bussing (1998), this is a lie-and-wait benthic predator, like others in the genus, that feeds on fishes and shrimps. It lurks under stones and overhanging shorelines. Winemiller and Morales (1989) found the diet comprised about 32% aquatic insect larvae, 39% shrimps and 9% fishes in Corcovado National Park, Costa Rica. The condition of seven specimens examined by Hildebrand (1938) suggested that spawning occurs during the dry season.

A single specimen of *Eleotris picta* was discovered during this study from San Juan de los Cayos, Falcon State, Venezuela. This is the first report of this species in the western Atlantic. It most likely resulted from introduction via ship's ballast water.

Eleotris pisonis (Gmelin, 1789)

Gobius pisonis, Gmelin, 1789:1206, South America (based on *Eleotris capite plagioplateo* of Gronow; after Marcgrave and Piso, Hist. Brasil, IV. 166, 1648; Brazil).

Gobius amorea Walbaum, 1792: 205, western Atlantic.

Eleotris gyrinus, Valenciennes, in Cuvier and Valenciennes, 1837: 220, pl. 356, Martinique and Saint-Domingue, (in part).

Eleotris (Culius) belizianus Sauvage, 1880: 56, Belize, (in part).

Eleotris carvalhonis Starks, 1913: 65, pl.9, Brazil.

DIAGNOSIS. 47-63 lateral scale rows, usually 50-54 in NE South America and 54-59 in Brazil. 2.3.4 suborbital free neuromast pattern. Spot on upper pectoral fin base lacking or poorly defined, not as dark as patch of pigment above opercle on edge of nape; no well-defined rows of spots or stripes on flanks

DESCRIPTION. Body morphology as described for genus. Both jaws with multiple rows of fine teeth, larger canines present laterally towards rear in outer row and/or medially near symphysis in inner rows. Proportional measurements are given in Table 4.

Meristics. First dorsal fin VI; second dorsal fin I, 8; pectoral fins 17 (15-19); pelvic fins I, 5; anal fin I, 8. Scales in lateral series 54 (47-63), usually 50-54 in Guianas and eastern Venezuela, 54-59 in Brazil; predorsal scales 40 (32-49); transverse scale rows 16 (14-20); caudal peduncle scale rows 17 (13 - 25).

Cephalic lateralis. Fig. 9. Five transverse suborbital free neuromast rows of which 2nd, 3rd and 4th extend ventrally beyond horizontal row *d* (2.3.4 pattern). Short supernumerary segments rarely observed. No *ot'* row on upper opercle, row *os* connects with row *oi* at lower rear margin of opercle.

Coloration in alcohol. Based on specimens from Brazil (AMNH 20743), Guyana (AMNH 14420, AMNH 72129, AMNH 72151), and Venezuela (MHNLS 9805, MHNLS 9945). Body tan to dark brown, often with a few scattered brown spots on upper flanks, not forming regular rows or thin stripes; dorsum occasionally lighter than flanks; abdomen and gular region lighter. Two streaks radiating across cheek posteriorly from eye, another along sulcus between nape and cheek and operculum, expanding into patch of dark brown pigment on nape along edge of operculum, more pronounced than pigment on upper pectoral-fin base. Spot or dark patch variably present on upper pectoral-fin base, if present not highly defined and not as dark as pigment on side of nape; other pigment as observed in *E. amblyopsis*.

DISTRIBUTION. Brazil to the Orinoco Delta of eastern Venezuela.

COMMENTS. *Eleotris pisonis* reaches a maximum size similar to *E. amblyopsis*. The largest we examined was a 113 mm SL individual from Brazil. Teixeira (1994) mentioned that this species was a common element of the ichthyofauna in estuaries of northeastern Brazil. The species was taken in salinities ranging from 0.1-18.2 ppt at temperatures of 25-33 C. It was most abundant in the fall in channels in regions of fluctuating salinity. Perrone and Vieira (1990) found that marginal vegetation served as the primary shelter and feeding area for this species in another Brazilian river system during the wet season.

Teixeira (1994) discovered *E. pisonis* primarily fed on snails (*Neritina virginea*), polychaetes, shrimps and fishes. *Neritina* were the principal food resource throughout the year; secondary foods changed with season and ontogeny. Smaller spinycheek sleepers ate polychaetes, larger individuals fed on fishes and shrimps. In another Brazilian estuary, this species ate mostly dipteran larvae in the wet season and carideans and fishes in the dry season (Perrone and Vieira, 1991). Seasonal changes in diet were associated with fluctuation in the abundance of marginal vegetation, a preferred habitat when it is present. As with the study by Teixeira, there were ontogenetic differences in diet. Juveniles fed mostly on dipterans, while adults ate more fishes and crustaceans.

Size at maturity for this species has been reported as 57 mm TL for males and 43 mm TL for females (Teixeira, 1994). He observed no clearly defined reproductive period for males, but noted an April surge for females. Perrone and Vieira (1990) gave a size at maturity of 35 mm SL for females (in agreement with that above) and suggested a reproductive period linked to the wet season, summer in southeastern Brazil and winter in the northeast.

Eleotris tecta, Bussing 1996

Eleotris tecta Bussing, 1996: 252, Rio Banegas, Puntarenas, Costa Rica.

DIAGNOSIS. Scales in lateral series 54-60, mode of 59. Neuromast configuration with 2nd, 3rd, and 4th suborbital rows extending ventrally past horizontal row *d*. Urogenital papillae round and blunt in females, long and acuminate in males.

DESCRIPTION. Body morphology as described for genus. Both jaws with multiple rows of fine teeth, larger canines present laterally towards rear in outer row and/or medially near symphysis in inner rows. Proportional measurements are given in Table 1.

Meristics. First dorsal fin VI; second dorsal fin I,8 (I,7- I,8); pectoral fins 17 (16-17); pelvic fins I, 5; anal fin I,8 (I,7-I,8). Scales in lateral series 59 (54-60), predorsal scales 38 (38-43); transverse scale rows 18 (17-21); caudal peduncle scale rows 14 (13-14).

Cephalic lateralis. Fig 2. Second, 3rd, and 4th suborbital vertical rows intersecting horizontal row *d* (2.3.4 pattern). No *ot'* row on upper opercle, opercular rows *os* and *oi* join at ventroposterior margin of preopercle.

Coloration in Alcohol. Based on specimens available. Body straw color, darker on dorsum, lighter on belly; mottling present in a few specimens; pigmentation

on lateral scales forming series of interrupted lines six to seven scales in depth extending from pectoral-fin base to caudal peduncle, more distinct posteriorly. Dark spot present on upper base of pectoral fin; dorsal and anal fins with wavy, dusky bands parallel or diagonal to body axis; bars on the caudal, pectoral, and pelvic fins perpendicular to body axis, some specimens lacking dusky bars on pectoral and pelvic fins. Cheek with small dark dots; interrupted interorbital bar; two postocular stripes, top stripe extends to the posterior margin of the opercle, bottom stripe extends to or slightly past the posterior margin of the preopercle; bar connecting two postocular stripes along seam of opercle and preopercle in a few specimens.

DISTRIBUTION. Pacific versant of Colombia, Panama and Costa Rica.

COMMENTS. Bussing (1998) stated that this species reaches 80 mm SL. The largest specimen we observed was 62 mm SL. The holotype of the species is female, not male as originally described by Bussing (1996). There was also some confusion in Figs. 2 and 3 of the original description. Cephalic neuromast drawings in Fig. 2 are from top to bottom *Eleotris picta* (c in legend), *E. tecta* (a in legend) and *E. tubularis* (b in legend). In Fig. 3, the illustrations are *Eleotris picta* in the upper left corner, *E. tecta* in the upper right and *E. tubularis* on the bottom.

From Bussing (1998) we know that *Eleotris tecta* inhabits streams with little to high current up to 75 m above sea level, and has been taken in waters with temperatures of 25-29 C. It is known to be sympatric, but not syntopic, with *E. picta*. He also stated that it is carnivorous.

Eleotris tubularis, Heller and Snodgrass, 1903

Eleotris tubularis Heller and Snodgrass, 1903: 210, Plate 10, Cocos Island, Costa Rica.

DIAGNOSIS. Scales in lateral series 48-53, mode of 50. Neuromast configuration with 2nd and 4th suborbital vertical rows extending ventrally past horizontal row *d*. Urogenital papilla round and blunt in females; urogenital papilla long and acuminate in males, tip extending past anal fin origin in adults; long pre-vent furrow.

DESCRIPTION. Body morphology as described for genus. Head is less robust than *Eleotris tubularis*. Proportional measurements given in Table 1.

Meristics. First dorsal fin VI; second dorsal fin I,8 (I,8-I,9); pectoral fins 16 (14-16); pelvic fins I, 5; anal fin I,8. Scales in lateral series 50 (48-53), predorsal

scales 36 (34-40); transverse scale rows 16 or 17(14-17); caudal peduncle scale rows 13 (12-16).

Cephalic lateralis. Fig. 2. Second and fourth suborbital vertical rows intersect horizontal row *d.* No *ot'* row on upper opercle, opercular rows *os* and *oi* do not meet at posterior opercular margin.

Coloration in Alcohol. Based on specimens available. Body olive brown with head region slightly darker; ventral surface lighter than dorsal surface. No dark spot on pectoral base; dorsal and anal fins with dusky bands parallel or diagonal to body axis; pectoral, pelvic, and caudal fins with dusky bars perpendicular to body axis.

Distribution. Endemic to Cocos Island, Costa Rica.

Comments. The holotype is desiccated but counts on measurements were taken where possible. This is also a small species, the largest individual observed in this study was 85 mm SL.

Materials Examined

Eleotris amblyopsis. Belize: FMNH 82078 (30); MNHN 27 (1), *Eleotris belizianus*, syntype; MNHN 2528 (2), *E. belizianus* syntypes. Brazil:AMNH 211135 (1); AMNH 20752 (1); Costa Rica: ANSP 140682 (1); ANSP 140683 (1); ANSP 174839 (2); ANSP 174841 (1); ANSP 174842 (1); NLU 69723 (8); Cuba: CAS 66647 (4); CAS 89139 (1); MCZ 32926 (2); MCZ 159203 (1). Florida: ANSP 71070 (5); ANSP 72915 (1); ANSP 72947 (1); ANSP 73105 (1); ANSP 144266 (1); MCZ 13435 (1); UF 59144 (5); UF 91947 (3); UF 87754 (1); UF 18133 (1); UF 47739 (1); UF 33977 (1); UF 87886 (8); UF 47003 (1). Guatemala: AMNH 32076 (3); AMNH 35114 (1). French Guiana: NLU 76503 (3); NLU 76504 (1); NLU 76505 (2); NLU 76506 (1). Guyana: FMNH 53923 (1); FMNH 53924 (1). Haiti: ANSP 83082 (1); AMNH 19315 (1); AMNH 19421 (1). Jamaica: CAS-SU 69780 (1). Louisiana: NLU 33488 (3); NLU 33614 (1); NLU 33958 (1); NLU 53287 (1); NLU 69722 (1); NLU 69736 (1); NLU 69843 (1); NLU 69844 (1); NLU 69845 (2); NLU 69846 (1); NLU 69851 (1); NLU 69852 (1); NLU 69853 (2); NLU 69854 (1); NLU 69900 (1); NLU 69901 (2); NLU 71488 (1). Mexico: CAS-SU 21122 (1); GCRL 2878 (6); UMMZ 167492 (1); UMMZ 178565 (3); UMMZ 184433 (4); UMMZ 184444 (3); UMMZ 184454 (1); UMMZ 238760 (1); UMMZ 184471 (1); UMMZ 184480 (8); UMMZ 184503 (2); UMMZ 184504 (1); UMMZ 186657 (1); UMMZ 194837 (23); UMMZ 194838 (4); UMMZ 194884 (2); UMMZ 196411 (14); UMMZ

194861 (4); UMMZ 209505 (5); UMMZ 209664 (1); UMMZ 209724 (2); UMMZ 209772 (2); UMMZ 213610 (1); UMMZ 213611 (3); UMMZ 213612 (9). Mississippi: GCRL 497 (2); GCRL 1456 (3): GCRL 2501 (20). North Carolina: UNC 8273 (1); UNC 10355 (5); UNC 11668 (1); UNC 14951 (6); UNC 15379 (1). Panama: ANSP 103393 (12); ANSP 104227 (1); ANSP 104291 (4); CAS 46149 (1); CAS-SU 50905 (1); CAS-SU 50317 (1); CAS 50318 (10); CAS-SU 50320 (5); CAS 214223 (1); (1); CAS 66651 (1); CAS 66652 (1). South Carolina: CAS-SU 2009 (1), *E. abacurus* holotype, specimen and radiograph. Surinam: AMNH 211136 (10); ANSP 10577-10579 (3), *E. amblyopsis* syntypes; CAS-SU 53292 (2); CAS-SU 53331 (5); MCZ 13429 (20); MNHN A.1672 (1), *E. gyrinus* syntype; MNHN A.1673 (3) *E. gyrinus* syntypes. Texas: TNHC 8115 (2). Trinidad: ANSP 144625 (1). Venezuela: CAS 50794 (2); ANSP 76244 (1); MCNG 19176 (1); MCNG 19245 (1); MCNG 13982 (1); SCN 1428 (11); SCN 1439 (1); SCN 1443 (4); SCN 1990 (1); SCN 9945 (1); SCN 14603 (3); SCN 14604 (2); SCN 14605 (1).

Eleotris annobonensis. Pagalu (Annobon): MNHN 1965.611 (4), paratypes; MNHN 1965.612 (4), paratypes; MNHN 1967.446 (1), holotype. Fernando Po: MRAC 7846p229 (1); MRAC 92089p0001-04 (4); MRAC 142100-01 (2); MRAC 7846p222-8 (7); MRAC 145418-20 (3).

Eleotris daganensis. Cameroun: MRAC 7302p2205-7 (3); MRAC 93083p0033-34 (2). Congo- Brazzaville: MRAC 8027p257-58 (2); MRAC 9057p2607 (1); MRAC 78027p256 (1). Gabon: MRAC 7660p126 (1). Guinea: MRAC 92059p4031 (1). Liberia: MRAC 7310p7385-91 (7); MRAC 7310p7392 (1); RMNH 24403 (6), *E. buttikoferi* paralectotypes. Namibia: RUSI 63257 (6). Nigeria: MRAC 8803p58-60 (3); MRAC 9019p529-33 (3); MRAC 9110p918-27 (10). Portuguese Congo: MRAC 1760 (1); MRAC 1764 (1). Rio Muni: MRAC 7846p235 (1); MRAC 173332-4 (3). Sierra Leone: MRAC 73406-8 (3); MRAC 73410-11 (2); MRAC 7310p7382-83 (2); MRAC 7310p7378-81 (4). Togo: MRAC 7313p429-31 (3).

Eleotris feai. Pagalu (Annobon): MNHN 1974.5.13.1 (1), paratype; MRAC 7445p1 (1), paratype.

Eleotris perniger. Bahamas: ANSP 98816 (1); ANSP 98817 (1); ANSP 148541 (1). Barbados: CAS-SU 37267 (7); MCZ 13283 (1). Bermuda: ANSP 150163 (1); ANSP 150164 (1). Brazil: ANSP 121269 (2); CAS-SU 69781 (1); MCZ 159204 (2). Cayman Islands: MCZ 52513 (1). Costa Rica: ANSP 163142 (1); ANSP 163772 (1); ANSP 163773 (2); ANSP 163774 (1); ANSP 163775 (2); NLU 69725 (4). Cuba: ANSP 39935 (1); ANSP 69214 (3); CAS-SU 1892 (3); CAS 66648 (2); MCZ 13342 (1); MCZ 13334 (1); MCZ 13355 (1); MCZ 13363 (1);

MCZ 13364 (4); MCZ 13366 (1); MCZ 13382 (1); MCZ 13384 (1). Dominican Republic: ANSP 10574 (1); MNHN A.1698 (3), *Eleotris gyrinus* syntypes. Florida: ANSP 55907 (1). Grenada: ANSP 52517 (3). Guadeloupe: MCZ 13440 (2). Haiti: ANSP 83082 (1); ANSP 83660 (1); CAS-SU 25604 (4). Honduras: CAS 35746 (1); GCRL 6003 (1); UF 16325 (6); UF 16333 (3). Jamaica: ANSP 112909 (1); ANSP 144716 (1); CAS-SU 4965 (8); MCZ 34030 (10); MCZ 58321 (8). Martinique: ANSP 152267 (1); MCZ 26070 (12); MNHN A.1597 (1), *E. gyrinus* syntype; NLU 75227 (3). Mexico: ECOCH (El Colegio de la Frontera Sur- Chetumal) 0243 (1); ECOCH 0505 (1); ECOCH 0573 (1); UMMZ 184467 (3); UMMZ 196529 (1); UMMZ 209702 (2). Panama: ANSP 99833 (3); ANSP 99915 (1); ANSP 104074 (6); ANSP 104096 (1); ANSP 104158 (2); ANSP 104302 (3); ANSP 104400 (5); CAS-SU 50277 (1); CAS 214224 (5); CAS-SU 50906 (5); CAS-SU 18578 (10); CAS-SU 18579 (11); CAS 66650 (1). Puerto Rico: ANSP 23552 (4); ANSP 23587 (1); ANSP 91914 (3); ANSP 115625 (1); ANSP 118559 (44); ANSP 144626 (3); CAS-SU 8243 (1); CAS-SU 8274 (2); CAS 78668 (2); CAS 11702 (1); MCZ 28871 (1); MCZ 34669 (1); MCZ 49411 (18). St. Martin: ANSP 10575 (1), *E. perniger* holotype. St. Vincent: MCZ 26103 (4); MCZ 26109 (1); MCZ 26111(11). Trinidad: ANSP 174843 (1). Venezuela: ex-MCNG 13982 (1); SCN 2451 (1); SCN 3958 (3); SCN 3966 (2); SCN 3968 (1); SCN 5969 (2); SCN 9245 (1); SCN 10001 (2); Virgin Islands: CAS 66645 (1); UMA (University of Massachusetts at Amherst) uncatalogued (1).

E. perniger x E. amblyopsis hybrids. Cuba: MCZ 13360 (2); MCZ 13365 (1); Mexico: ECOCH 0272 (1); ECOCH 0861 (1); UMMZ 124299 (1). Panama: ANSP 178003 (1); MCZ 45744 (1).

Eleotris picta. Colombia: NRM 28607 (1); NRM 28609 (1); NRM 10704 (1); FMNH 94689 (15); CAS 11691 (1); LACM 24320 (1); NRM 39516 (3); NRM 10705 (2). Costa Rica: ANSP 144126 (1); ANSP 144155 (5); ANSP 144132 (15); LACM 30109-5 (2); LACM 2887 (3); LACM 4859 (1); TNHC 15362 (5); TNHC 14789 (3); TNHC 15380 (1); TU uncat. (2); TU 84587 (1); TU 24181 (1); TU 84544 (1); TU 84687 (1); TNHC 14849 (5); TNHC 15350 (3); TNHC 11986 (1); TNHC 12006 (1); TNHC 11496 (1); TNHC 11505 (1); TNHC 15360 (1); TNHC 14755 (2); UCR 130.003 (12); UCR 936.006 (5); UCR 732.007 (5). Isla del Cocos, Costa Rica: LACM 26462 (2); UCR 736.005 (2). Ecuador: MCZ 58605 (1); MCZ 54970 (1); USNM 288041 (2); CAS 66643 (2); FMNH 56864 (2); CAS 66644 (1); FMNH 56865 (1). Ecuador, Galapagos Islands: UWZM 10688 (1); CAS 54585 (1); SIO 59-358-58B (1); LACM 43964-1 (1). Guatemala: UMMZ 194134 (3); UMMZ 197122 (1); UMMZ 188085 (5); UMMZ 190541 (2). Honduras: TU 186087 (1). Mexico: UMMZ 164635 (1); LACM 30369-2 (1); UMMZ 164646 (1); UMMZ 173605 (1); CAS-SU 2907 (5); UMMZ 164627 (1); UMMZ 164685 (1); UMMZ 172012 (1); UMMZ 172096

(1); UMMZ 172060 (3); UMMZ 183927 (1); UMMZ 172082 (1); UMMZ 183935 (1); UMMZ 172145 (1); UMMZ 184827 (5); UMMZ 184747 (1); UMMZ 178428 (1). Nicaragua: UCR 52.002 (10); UCR 272.003 (1); UCR 187.002 (7); UCR 270.006 (20). Panama: NMW 76866 (1), *E. picta* syntype; FMNH 27274 (1); FMNH 27280 (7); ANSP 146763 (1); USNM 226407 (2); FMNH 32313 (1); FMNH 32312 (1); FMNH 27283 (6); FMNH 27281 (3); FMNH 32314 (1); ANSP 104276 (2); ANSP 104277 (1); ANSP 104282 (1); ANSP 104189 (1); ANSP 104101 (1); ANSP 104403 (2); CAS 66637 (1); CAS 66638 (1); FMNH 27275 (1); ANSP 104165 (2); FMNH 36985 (1); USNM 270831 (10); USNM 260093 (3); USNM 293478 (4); NRM 35870 (1). Venezuela: SCN 2270 (1).

Eleotris pisonis. Brazil: AMNH 3764 (1), *Eleotris carvalhonis*, paratype; AMNH 20743 (2); ANSP 69641 (1); CAS-SU 22208 (5), *E. carvalhonis* paratypes; CAS-SU 22215 (1), *E. carvalhonis* holotype, specimen and radiograph; CAS 39109 (3); CAS-SU 52355 (15 of 62); CAS-SU 52356 (2); CAS-SU 52359 (1); CAS-SU 52360 (1); CAS 53478 (1); MCZ 1196 (1); MCZ 4627 (1); MCZ 13385 (1); MCZ 13386 (1); MCZ 13389 (2); MCZ 13391 (1); MCZ 13397 (5). French Guiana: MNHN A.2216 (3), *Eleotris belizianus* syntypes; MNHN A.2217 (5), *E. belizianus* syntypes. Guyana: AMNH 14420 (1); AMNH 72049 (1); AMNH 72129 (7); AMNH 72151 (1); AMNH 73056 (1); AMNH 14420 (1); CAS 51066 (1). Surinam: AMNH 54793 (31); MNHN A.1693 (1), *E. gyrinus* syntype. Venezuela: ANSP 149479 (1); SCN 1429 (7); SCN 1962 (1); SCN 9805 (11); SCN 13142 (4); SCN 13485 (2); SCN 14602 (2).

Eleotris senegalensis. Cameroun: MRAC 7302p2208-09 (2); MRAC 7329p1630-31 (2). Congo: AMNH 17020 (1). Congo-Brazzaville: MNHN 1901.8.1.90-3 (1); MRAC 9057p2612-15. Gabon: MRAC 7302p2204 (1); MRAC 7660p125 (1). Guinea: MRAC 92059p4032-33 (2). Liberia: MRAC 7310p7567-68 (2); RMNH 5254 (1), *E. buttikoferi* lectotype. Nigeria: MRAC 9263p357-8 (2); MRAC 8608p42 (1); MRAC 9110p928 (1). Senegal: MRAC 771p640 (1). Sierra Leone: MRAC 7310p7556 (1).

Eleotris tecta. Colombia: NRM 43549 (1); CAS 66639 (1); CAS-SU 37538 (2); CAS-SU 37539 (2). Costa Rica: LACM 45893-1 (1), *E. tecta* holotype. Panama: USNM 357288 (3).

Eleotris tubularis. Isla del Cocos, Costa Rica: CAS-SU 6348 (1), *E. tubularis* holotype; LACM 25806 (23); LACM 20047 (20).

Eleotris vittata. Angola: AMNH 223211 (1); BMNH 1864.7.11.8 (1), *E. monteiri* type. Benin: MRAC 8958p15 (1). Cameroun: MRAC 7308p26 (1). Congo:

AMNH 43132 (2). Congo- Brazzaville: MRAC 9057p2416-17 (2). Cote D'Ivoire: MRAC 173598 (1). Fernando Po: MRAC 142099 (1). Gabon: MNHN a.1548 (1). Liberia: MRAC 7310p7384 (1). Nigeria: MRAC 8843p463-5 (3); MRAC 8803p56-57 (2); MRAC 9022p4 (1). Sierra Leone: MRAC 7310p7382-83 (2). Togo: MRAC 739p141 (1).

Erotelis armiger. Mexico: CAS-SU 3455 (1), *Alexurus armiger* holotype, specimen and radiograph.

Erotelis smaragdus. Florida: CAS 51044 (1). Louisiana: UNOVC (University of New Orleans Vertebrate Collections) 4295 (1). Panama: CAS-SU 19339 (2).

Acknowledgments

Specimens were provided by W. G. Saul and M. Sabaj (ANSP), M. Stiassny and B. Brown (AMNH), A-M. Hine (BMNH), D. Catania and W. Eschmeyer (CAS), J. J. Schmitter-Soto (ECOCH), B. Chernoff and M.A. Rogers (FMNH), S. Poss (GCRL), J. Seigel and C. Thacker (LACM), D. Taphorn (MCNG), K. E. Hartel (MCZ), O. M. Lasso-Alcala (SCN), D. Nelson (UMMZ), J.-C. Hureau, P. Keith and P. Pruvost (MNHN), G. Teugels and M. Parrent (MRAC), S. Kullander (NRM), H. Wellendorf (NMW), M.J. P. van Oijen (RMNH), V. Mthombeni and R. Bills (RUSI), C. Klepadlo (SIO), D. Hendrickson, M. Leslie and A. Rentz (TNHC), H. Bart, N. Rios and M. Taylor (TU), W. Bussing (UCR), C. Gilbert, G. Burgess and R. Robins (UF), D. Smith (UMA), D. W. Nelson (UMMZ), R. Cashner and M. O'Connell (UNOVC), F. Swartz (UNC), S. L. Jewett and L. Palmer (USNM), and J. Lyons (UWZM). We thank M. Gambordella for lab assistance and L. Olsan for Latin translations.

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Table 1. Eastern Pacific *Eleotris* morphometric data. Standard length reported to nearest 0.1 mm. P1 = pectoral fin, D2 = second dorsal fin. Orbit, interorbital, snout and upper jaw measurements expressed as per cent of head length, all others expressed as per cent of standard length (all rounded to nearest per cent).

	Eleotris picta			*Eleotris tecta*			*Eleotris tubularis*		
character	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range
standard length	95.9 (255)	89.9-101.9	30.5-276.0	47.9 (8)	41.5-54.4	37.0-61.6	60.5 (45)	56.6-64.3	31.6-85.0
orbit length	19 (255)	18-19	11-37	22 (8)	21-24	20-24	24 (45)	23-24	21-28
snout length	22 (255)	21-22	7-28	22 (8)	21-24	19-25	25 (45)	24-25	19-30
interorbital width	27 (255)	26-27	16-37	25 (8)	21-29	18-32	28 (45)	26-29	20-26
upper jaw length	42 (255)	41-42	30-52	43 (8)	41-45	39-46	48 (45)	47-49	42-54
head length	29 (253)	29-30	25-34	27 (8)	26-28	24-30	29 (45)	28-29	22-32
head width	21 (253)	20-21	12-36	18 (8)	17-19	16-20	22 (45)	21-22	16-26
predorsal length	41 (253)	41-42	20-46	40 (8)	34-46	23-45	41 (45)	41-42	31-44
nape depth	16 (253)	16	11-22	15 (8)	14-16	13-17	18 (45)	18-19	12-22
body width P1 base	17 (253)	17-18	10-26	17 (8)	16-18	15-18	19 (45)	18-20	13-37
body width D2 origin	13 (253)	13	8-17	12 (8)	11-13	10-14	14 (45)	13-14	8-17
preanal length	58 (253)	57-58	48-64	56 (8)	55-57	55-59	55 (45)	54-56	43-59
postanal length	44 (253)	44	30-54	45 (8)	44-46	44-48	46 (45)	45-47	35-49
caudal peduncle length	25 (253)	25-26	18-32	26 (8)	24-28	22-29	26 (45)	26-27	24-29
pectoral fin length	22 (254)	21-22	15-29	23 (8)	19-28	19-36	24 (45)	23-24	19-26
pelvic fin length	16 (253)	16	12-21	17 (8)	14-21	14-28	17 (45)	17-18	12-20
caudal fin length	25 (253)	25	16-30	22 (8)	21-24	20-24	24 (43)	23-24	20-26

Table 2. Meristic characters for eastern Pacific *Eleotris*. Means and 95% confidence interval values rounded to the nearest whole number. Cpd = caudal peduncle scale rows. P1 = pectoral fin.

	Eleotris picta				*Eleotris tecta*				*Eleotris tubularis*			
character	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode
cpd scales	19 (255)	19	16-24	18	14(8)	13-14	13-14	14	14(45)	13-14	12-16	13
lateral scales	62(255)	61-62	56-66	61	59(8)	57-60	54-60	59,60	50(45)	49-50	48-53	49
transverse scales	25(255)	24-25	20-31	24	18(8)	17-19	17-21	18	16(45)	16	14-17	16,17
predorsal scales	61(255)	60-61	53-65	61	38(8)	38-43	38-47	38	37(45)	36-37	34-40	37
left P1 rays	18(255)	18	11-19	18	17(8)	16-17	16-17	17	16(45)	15-16	14-16	16

Table 3. Geographic patterns of meristic variation in *Eleotris picta*. Regions are: 1) Baja California - Puerto Vallarta, Mexico, 2) Puerto Vallarta, Mexico - Guatemala Border, 3) Guatemala, Honduras, El Salvador, Nicaragua, 4) Costa Rica, Panama 5) Colombia, Ecuador, Galapagos Islands.

REGION	MEAN	LOW 95% CI	UP 95% CI	MODE
		LATERAL SCALES		
1	63.00	61.97	64.03	65
2	63.00	61.92	64.08	64
3	61.72	61.26	62.18	61
4	61.18	60.90	61.46	60
5	61.95	61.44	62.47	61
		PREDORSAL SCALES		
1	60.63	59.31	61.94	62
2	60.09	58.11	62.07	62
3	60.34	59.84	60.84	60
4	60.29	59.97	60.60	61
5	61.51	60.95	62.08	61
		TRANSVERSE SCALES		
1	23.25	22.39	24.11	24
2	24.91	24.28	25.54	25
3	26.02	25.41	26.63	25
4	24.56	24.26	24.85	25
5	24.15	23.71	24.59	24
		CAUDAL PEDUNCLE SCALES		
1	18.31	17.85	18.78	18
2	19.18	18.34	20.02	19
3	19.70	19.24	20.16	19
4	18.59	18.40	18.78	19
5	18.15	17.78	18.51	17,18
		PECTORAL FIN RAYS (LEFT)		
1	17.56	17.29	17.84	18
2	17.82	17.55	18.09	18
3	17.74	17.59	17.89	18
4	17.66	17.53	17.80	18
5	17.36	17.18	17.55	17

Table 4. Western Atlantic *Eleotris* morphometric data. Standard length reported to nearest 0.1 mm. P1 = pectoral fin, D2 = second dorsal fin. Orbit, interorbital, snout and upper jaw measurements expressed as per cent of head length, all others expressed as per cent of standard length (all rounded to nearest per cent).

	E. amblyopsis			*E. perniger*			*E. pisonis*		
character	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range	Mean (N)	95% C.I.	Range
standard length	48.2 (342)	46.0 - 50.3	10.9 - 112.6	66.7 (251)	66.7 - 75.3	14.6 - 176.6	58.4 (146)	54.8 - 62.0	17.2 - 112.7
orbit length	19 (137)	19 - 20	14 - 25	19 (70)	18 - 20	13 - 26	18 (55)	18 - 19	14 - 24
snout length	21 (63)	20 - 21	15 - 26	22 (56)	21 - 22	16 - 27	22 (40)	22 - 23	19 - 28
interorbital width	25 (55)	23 - 27	12 - 36	26 (54)	24 - 28	16 - 35	27 (45)	26 - 28	20 - 35
upper jaw length	39 (67)	38 - 40	31 - 48	42 (60)	40 - 43	33 - 51	42 (49)	41 - 43	33 - 49
head length	32 (137)	32 - 32	27 - 36	31 (70)	31 - 31	27 - 36	31 (55)	31 - 32	28 - 34
head width	21 (51)	20 - 21	16 - 26	22 (47)	21 - 23	16 - 31	21 (38)	20 - 21	16 - 27
predorsal length	43 (83)	42 - 43	30 - 49	43 (45)	43 - 44	39 - 42	42 (39)	41 - 43	38 - 46
nape depth	14 (51)	13 - 15	8 - 21	14 (45)	13 - 15	8 - 24	15 (37)	14 - 17	8 - 23
body width P1 base	16 (51)	15 - 16	9 - 19	17 (44)	16 - 18	11 - 26	17 (37)	17 - 18	13 - 20
body width D2 origin	11 (50)	11 -12	8 - 15	13 (45)	12 - 14	6 - 17	13 (37)	12 - 14	9 - 18
preanal length	57 (50)	56 - 58	41 - 65	59 (41)	58 - 60	53 - 64	57 (37)	56 - 57	54 - 61
postanal length	44 (50)	43 - 44	40 - 48	42 (41)	42 - 43	38 - 46	44 (37)	43 -44	40 - 47
caudal peduncle length	25 (50)	24 - 26	19 - 33	25 (41)	24 - 25	22 - 27	25 (37)	25 - 26	21 - 28
pectoral fin length	26 (136)	25 - 26	19 - 31	25 (70)	24 - 25	20 - 35	23 (55)	23 - 24	20 - 26
pelvic fin length	20 (135)	20 - 21	12 - 26	18 (72)	18 - 19	14 - 25	18 (55)	18 -18	15 - 22
caudal fin length	29 (49)	28 - 30	13 - 33	26 (34)	26 - 27	22 - 31	27 (41)	26 - 27	20 - 31

Table 5. Meristic characters for western Atlantic *Eleotris*. Means and 95% confidence interval values rounded to the nearest whole number. Cpd = caudal peduncle scale rows, P1 = pectoral fin.

	E. amblyopsis				*E. perniger*				*E. pisonis*			
character	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode	mean (N)	95% C.I.	Range	Mode
cpd scales	15 (53)	14-16	11-24	12	17 (46)	16-18	13-21	17	17 (45)	16-18	13-25	15
lateral scales	49 (316)	48-49	40-58	52	60 (235)	60-61	54-68	60	54 (139)	53-54	47-63	51,53
transverse scales	14 (53)	14-15	11-18	15	20 (48)	20-21	17-23	20	16 (44)	16-17	14-20	17
predorsal scales	36 (60)	35-37	29-46	33-35,39	49 (52)	47-50	39-62	47	40 (49)	39-42	32-49	40
left P1 rays	17 (161)	17	15-18	17	18 (104)	18	16-19	18	17 (71)	17	15-19	18

Table 6. Geographic affinities of West African genera of gobioid fishes. (* Introduced)

West African Endemic	South African Endemic	Western Hemisphere	Northeast Atlantic/ Mediterranean	Indo-Pacific	Global
Hannoichthys	*Caffrogobius*	*Dormitator*	*Gobius*	*Bostrychus*	*Eleotris*
Kribia	*Psammogobius*	*Ctenogobius*	*Leseuerigobius*	*Prionobutis**	*Awaous*
Ebomegobius		*Gobioides*	*Mauligobius*	*Parasicydium*	*Bathygobius*
Gorogobius		*Gobionellus*	*Thorogobius*	*Periophthalmus*	*Gnatholepis*
Nematogobius		*Sicydium*			*Priolepis*
Porogobius					
Wheelerigobius					
Yongeichthyes					

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